

THE ECOLOGY OF THE ARCTIC CHAR AND DOLLY VARDEN
IN THE BECHAROF LAKE DRAINAGE, ALASKA

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A
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Abstract

Becharof Lake is home to both Arctic char (*Salvelinus alpinus*) and the closely related Dolly Varden (*Salvelinus malma*), two species known not only to be similar in appearance but also to exhibit similar life histories. The body morphometry, otolith microchemistry, and stomach contents of both species were studied in fish collected from May to September 1998. Morphometric and meristic analysis revealed clear separation in body structure between the two species, as well as potential sub-populations within each species. Otolith microchemistry revealed incidences of anadromy and non-anadromy in both species. Stomach content analysis revealed a broad feeding niche but smaller ranges in food types in individual Arctic char with little seasonal preference, whereas Dolly Varden showed seasonality in food choices. Data suggest that both species can move in and out of the lake system, and that little competition for food or habitat occurs between the two species in the summer months.

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Introduction

The Arctic char (*Salvelinus alpinus*) is the northernmost freshwater fish in the world, found as far north as Ellesmere Island, Northwest Territories, Canada (82°N) (Babaluk et al. 1997; Morrow 1980). It is also circumpolar species that can exhibit both anadromous and strictly freshwater life history patterns (Babaluk et al. 1997; Halden et al. 1995; Chernitsky 1990; Morrow 1980). In addition, it has been reported that in large, deep, oligotrophic lakes, up to four morphologically distinct forms can develop sympatrically, occupying different niches in the lake system (Reist et al. 1995; Sandlund et al. 1992; Hammar 1990; Saavaitova 1990). Chereshev and Skopets (1990) reported the presence of three species (including one new genus) of char in Lake El'gygytyn in northern Russia. Two species, the boganid char (*Salvelinus boganidae*) and the smallmouth char (*Salvelinus elgyticus*), appear to have developed sympatrically from similar ancestry, while the third species (and new genus), the longfin char (*Salvethymus svetovidovi*), appears to be an endemic fish that probably developed in the lake from about 3-4 million years ago during the Miocene (Glubokovsky and Frolov 1994). All three species inhabit different niches in the lake system: the longfin char appears to be a benthic feeder of invertebrates, the smallmouth is a planktivore inhabiting the pelagic zone, and the boganid feeds primarily on the other two (F. DeCicco, Alaska Department of Fish and Game, Fairbanks, personal communication).

In some systems, the Arctic char may coexist with the closely related Dolly Varden (*Salvelinus malma*) (Delacy and Morton 1943). In North America, the Dolly

Varden exists in at least two taxonomic forms: a northern form that occurs from the Mackenzie River in the Yukon Territory south to the north-draining systems on the Alaska Peninsula, and a southern form that occurs from the south-draining systems on the Alaska Peninsula south to northern California (DeCicco 1989; Morrow 1980). The northern form Dolly Varden typically has 21-23 gill rakers and 25-30 pyloric caeca, while the southern form has 16-18 gill rakers and 20-30 pyloric caeca (Behnke 1980). The southern form Dolly Varden is usually associated with lakes or lake/river environments, whereas the northern form tends to utilize only streams and rivers in freshwater; and is commonly anadromous (DeCicco 1989; Morrow 1980). McPhail (1961) reports that the northern and southern forms of Dolly Varden probably originated from a single population that was divided by glaciation. The northern form may have evolved in the unglaciated coastal areas of Alaska and Siberia, while the southern form may have evolved to the south of the ice sheet. Unlike other anadromous Pacific salmonids, Dolly Varden exhibit movement to multiple drainages, with tagged fish from northwestern Alaska recaptured as far away as the Anadyr River in Russia, a movement of over 1690 km (DiCicco 1992).

In systems where both Arctic char and Dolly Varden are found, there has been much difficulty distinguishing between the two. Dolly Varden can usually be distinguished externally from Arctic char by their blunter snout and by the smaller spots on their body (normally smaller than the diameter of the pupil), and internally by their smaller numbers of gill rakers and pyloric caeca (Stolz and Schnell 1991; Morrow 1980). Dolly Varden also typically have a more laterally compressed body

(possibly an adaptation to living primarily in running waters), while the Arctic char body is more rounded and fusiform. Reist et al. (1997; 1990) used an extensive suite of morphometric and meristic measurements in addition to allozyme and polymorphic enzyme data to distinguish between the two species, as well as to differentiate races within species. The molecular approaches may be particularly helpful in systems where both Arctic char and Dolly Varden are found, for convergence in phenotype may occur along with hybridization or introgression (J. Reist, Canadian Department of Fisheries and Oceans-Winnipeg, personal communication).

Environmental factors (e.g., lake productivity, inter- and intraspecific competition, ease and distance of migration) affecting fish growth and fecundity are likely the key factors in determining the degree of anadromy (Kristoffersen et al. 1994). Freshwater parasites may influence the degree of anadromy. Dick and Beloslevic (1980) suggested that a severe infection with *Diphyllbothrium spp.* has a negative impact on the likelihood of anadromy behavior in salmonids, but Kristoffersen et al. (1994) found that severe infection with *Diphyllbothrium spp.* did not affect the degree of anadromy in Norwegian Arctic char populations.

In Becharof Lake, a large, deep, remote lake on the Alaska Peninsula, both Arctic char and Dolly Varden are found, but very little research has been done on the chars of this system, except for occasional research on abundance and movement on the Dolly Varden in select inlet streams (J. Adams, USFWS, King Salmon, personal communication). Given the immense size (1200 km²), depth (>150 m in some places), large number of potential food resources, and remoteness of Becharof Lake, I

hypothesized that there existed the possibility of Arctic char and Dolly Varden with multiple life history strategies, including anadromy and non-anadromy. There was also the potential for morphological variation within strictly lacustrine populations.

Mathisen and Farley (1995) reported returns of 3 to 25 million salmon/year into Becharof Lake for the period 1988-1994, with about 8 recruits returning for each spawner in some years. A comprehensive study of the life history of Arctic char and Dolly Varden (known predators of salmon smolt and eggs) in Becharof Lake could enhance our baseline knowledge of the fish community and trophic ecology in this commercially important system. Compared to other vertebrates, evolutionary changes in char populations may be especially rapid, and would therefore make chars excellent subjects for studies of microevolution and phenotypic variation (Saavaitova 1990). In addition, chars are typical representatives of northern freshwaters and can serve as indicators of the health of high latitude ecosystems (Saavaitova 1990).

Morphometrics and Meristics

Size and shape information of body morphology can provide fundamental clues into relationships among organisms, and used in conjunction with genetic data can provide a sound basis for classification of groups or individuals (Reist 1985). Morphometric measurements (the dimensional measures of the body and body parts) and meristic characters (counts of repeated body structures or segments) have become increasingly important in studies of the external phenotype of organisms, particularly where questions of species classification are present.

In some systems, morphotypes of chars may be determined rather well on the basis of morphological characters. Throughout its circumpolar distribution, chars may show extensive phenotypic variation, both among and within drainages, with up to four distinct morphs in the same system (Nikoslkii 1969; Behnke 1972, 1980, 1984). These differences among sympatric morphs may include: coloration, meristic characters, growth rate, size and age at sexual maturity, time and place of spawning, food and habitat choice, and parasitic infection rate (Johnson and Burns 1984; Sandlund et al. 1992). DeLacy and Morton (1942) used comprehensive morphometric and meristic data in conjunction with tagging and stomach content data to separate Dolly Varden from the "red lake" or "alpine" char (likely a regional name for Arctic char) in the Karluk Lake drainage on Kodiak Island, Alaska. McPhail (1961) used morphometric and meristic information to generate a discriminant function that quantified clear differences between Dolly Varden and Arctic char in the Karluk and Fraser rivers on Kodiak Island; he concluded that there may be at least two distinct forms of both species in North America. More recently, Reist et al. (1995) used extensive morphometric and meristic information to demonstrate the presence of two distinct forms of Arctic char in Lake Hazen, Ellsmere Island, Northwest Territories. Analyzing these data using multivariate and covariate techniques, morphological differences between groups within species and between closely related species can be tested for statistical significance, and can aid in the proper classification of individuals into their respective groups (Reist 1985).

Otolith Microchemistry

Otolith microchemistry has been used to determine anadromous behavior in chars, whitefishes, and other species. Evidence of strontium deposition in place of calcium has been shown to be a definitive indicator of anadromy (Radtke et al. 1996; Halden et al. 1995; Reist et al. 1995). Arctic char and Dolly Varden that migrate out to sea to feed may experience faster growth rates, earlier reproductive age, and higher fecundity (Radtke et al. 1996; Foy 1996). Moyle and Cech (1996) reported that a 500 g rainbow trout *Oncorhynchus mykiss* that has lived in a stream for four years will typically produce fewer than 1000 eggs, whereas a 4 kg anadromous trout (steelhead) of the same age can produce 4000 or more eggs. By becoming anadromous, these fish may take advantage of the more abundant food resources found in saltwater than in most oligotrophic lakes (such as Becharof Lake), then return to freshwater to reproduce and overwinter.

Otoliths are composed mainly of needle-shaped crystals of calcium carbonate radiating outwards in three dimensions from a nucleus and passing through a network of organic material (Moyle and Cech 1996). The otolith grows as more material in the form of new crystals is deposited on outer surfaces. Because otoliths do not undergo absorption, they are good records of age and have been shown to contain a permanent record of strontium (Sr). The calcium, strontium, and other trace elements that are deposited are derived mainly from the waters in which the fish live. Seawater contains, on average, 8.0 mg/L Sr, whereas freshwater contains only 0.1 mg/L Sr (Rosenthal et al. 1970). These differences in Sr concentrations are reflected in otolith

composition (Radtke et al. 1990). Calcium and strontium are similar in that they have the same atomic configuration (two valence electrons), but strontium may be preferentially deposited on the otolith because it has more than twice the atomic mass ($83\mu\text{g/mol}$) of calcium ($40\mu\text{g/mol}$). The concentration of strontium in otoliths can therefore provide a distinct and unambiguous marker for fishes migrating between marine and freshwater systems. Babaluk et al. (1997) used a scanning proton microprobe to detect strontium deposition in otoliths of Arctic char caught from several different locations in the Canadian Arctic, and found that anadromous fish showed low, relatively consistent strontium deposition in for the first several years of their lives, followed by sharp, oscillatory peaks and valleys (up to 2000 ppm), corresponding to yearly migrations to sea after their sixth year (smoltification). Known non-anadromous fish showed low, consistent strontium deposition throughout their lives (100-300 ppm), even in Arctic char as old as 23 years.

Stomach Content Analysis

The Arctic char is usually described as a generalist feeder with a broad feeding niche, having a wide-ranging and opportunistic diet (Amundsen 1995; Johnson 1980). However, within this broad population feeding niche, smaller, narrower individual feeding niches may develop (Amundsen 1995). Optimal forage theory predicts that with abundant food resources the search time is low, and the predators can afford to be selective and specialize on the superior prey type (Diana 1995). Conversely, if food supply is restricted and the encounter rate is low, a predator cannot afford to bypass many inferior prey items, and generalization is

promoted. Arctic char may also be highly responsive to seasonal food availability, and therefore fish collected at different times from the same site may switch to feeding on something totally different. Amundsen (1995) reported seasonal variation in the feeding niche of a lacustrine Arctic char population in Norway, largely related to summer production of chironomid pupae (the preferred food type when available, with sticklebacks, zooplankters, and mollusks becoming more important in the colder months). Using stomach content data alone to quantify niche separation could prove difficult, particularly if the sampling gear consists of gill nets, fyke nets, hoop traps, or other gear that could enable the fish to digest food between the time of first encountering the gear and removal from the gear. However, using trends in stomach contents to support morphometric/meristic and otolith microchemistry information could help describe trends in habits and movement.

Study Objectives

The purpose of this study was to investigate differences in morphology and ecology of Arctic char and Dolly Varden, and to determine if any within-species morphological differentiation and food and/or habitat specialization occurs within the system. To fulfill this purpose, my objectives were to:

1. Sample Arctic char and Dolly Varden from different habitats within the lake and collect comprehensive morphological and meristic data from each fish as described by Hammar (1990) and Reist (1990) to test for within-system variation;

2. Use scanning proton microprobe technology to determine if life histories include anadromy;
3. Conduct stomach content analysis of each fish to test for correlations with respect to any within-species and between-species differences in habitat or morphology.

Study Area

Becharof Lake is the second largest lake in Alaska, and excluding the Laurentian Great Lakes, is the third largest freshwater lake in the United States. It is located on the Alaska Peninsula almost wholly within the Becharof National Wildlife Refuge in southwestern Alaska (Figure 1). The lake is approximately 1200 km², and has approximately 30 inlet streams that drain into the lake, about half of which are large enough to support runs of sockeye salmon (*Oncorhynchus nerka*). The lake is classified as oligotrophic, with calcium bicarbonate-chloride chemistry (LaPerriere 1998). The lake is somewhat unusual in that it is intersected by a large fault that degasses magmatic carbon dioxide, particularly in an area called the Gas Rocks. All the inlet streams are derived from hyporheic flow or snowmelt save for one, the Kejulik River, which is primarily glacial in origin. The outlet river, the Egegik, consists of about 65 km of Class I water, and would therefore be an easy migration corridor for anadromous fishes. The lake is fed by the Ruth River at the southeast corner (which drains Ruth Lake, both of which were included in the sampling because they are so closely connected to Becharof Lake). Becharof Lake is deep (183 m at the deepest recorded spot and an estimated mean depth of 56 m) and does not appear to

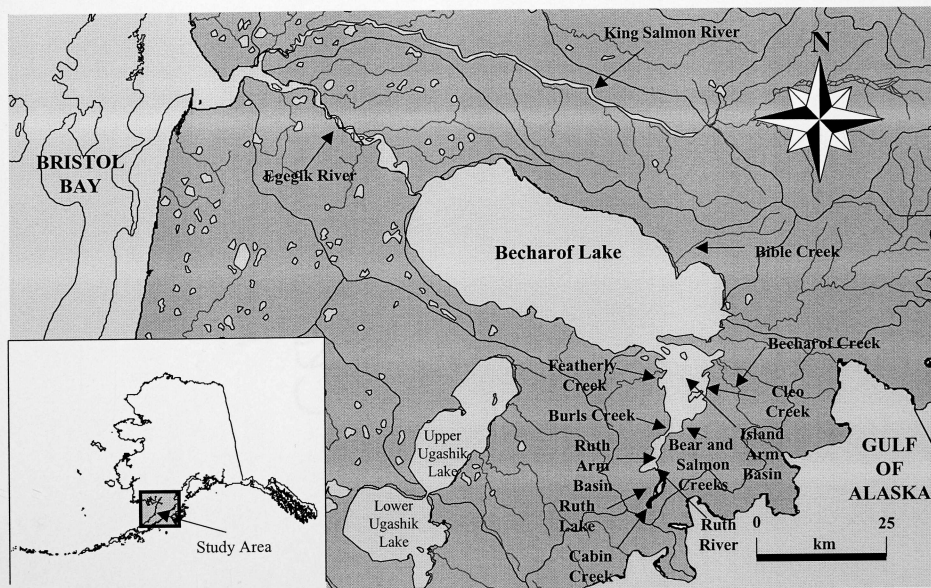


Figure 1. The Becharof Lake drainage.

stratify thermally in summer, likely due to mixing by frequent storms and wind events. The system supports the second largest run of sockeye salmon in Bristol Bay, with annual escapements of well over one million fish. Other species present include coho salmon (*Oncorhynchus kisutch*), three-spined stickleback (*Gasterosteus aculatus*), nine-spined stickleback (*Pungitius pungitius*), round whitefish (*Prosopium cylindraceum*), lake whitefish (*Coregonus clupeaformis*), pygmy whitefish (*Prosopium coulteri*), Bering cisco (*Coregonus laurettae*), northern pike (*Esox lucius*), and slimy sculpin (*Cottus cognatus*).

Methods

Fish Collection

Arctic char and Dolly Varden were collected from various localities in the Becharof Lake drainage from May 1998 through September 1998. Sampling began on the outlet river, the Egegik, during the last two weeks of May. It is about this time that a massive outmigration of sockeye salmon smolts occurs, and information from the Alaska Department of Fish and Game, Commercial Fisheries Division, suggested that at least one of these species gathers at the outlet just down from the lake to feed on the smolts. During May 17-29, 33 fish (17 Arctic char, 16 Dolly Varden) were caught using hook-and-line gear. Unusually cool water was not conducive to smolt movement, and therefore the outmigration did not commence during our sampling. It is likely our catches would have been higher if smolts were actively moving.

In June, we began gill netting the lake in various habitats including littoral, pelagic, profundal, and benthic zones. The strategy was not to catch as many fish as

possible, but to sample all potential habitats. The sampling gear consisted of two Swedish-style, variable mesh, nylon experimental nets. One net consisted of six 20-m panels, with bar mesh sizes from 10 mm to 25 mm. The other net consisted of six 20-m panels, with bar mesh sizes from 10 mm to 60 mm. By using both nets, we attempted to normalize the length distribution of the catch, and get a better representative of the length composition of the population. Small mesh nets can catch both small fish (by the gills and fins mostly) and large fish (their mouths and maxillaries can be easily caught in them, and they may be attracted to smaller fish writhing in the net) whereas large mesh catches primarily larger fish only. Therefore, we tried to overrepresent the smaller mesh in attempt to equalize capture probabilities between length classes.

In attempt to capture more Dolly Varden (we caught only one juvenile Dolly Varden in nets all summer), we sampled inlet streams via hook and line. Dolly Varden were collected from nine inlet streams: Salmon Creek, Bear Creek, Cleo Creek, Cabin Creek, Becharof Creek, Burls Creek, Bible Creek, Featherly Creek, and the Ruth River (Figure 1).

Lake and inlet sampling consisted of two sampling periods: June 5 to July 9, and again from August 5 to September 10. A total of 156 Arctic char and 64 Dolly Varden were sampled during these periods, for a total of 173 Arctic char and 80 Dolly Varden sampled for the season.

Morphometric/Meristic Data Collection

The comprehensive morphometric and analysis was designed by Reist et al. (1995; 1990); 19 morphometric measurements and 8 meristic counts were obtained from each fish (Figure 2). All fish were sampled within hours of capture. Meristic counts consisted of principal ray counts for pectoral (PRC), dorsal (DRC), ventral (VRC), and anal (ARC) fins. Counts of branchiostegal rays (BRC), upper (UGR) and lower gill rakers (LGR) and pyloric caecae were also made.

Morphometric measurements were made in the field using hand-held calipers, with all measurements made to the nearest 0.1 mm. As described by Reist et al. (1995), the body was divided into areas defined by particular features and the size of the part to be measured. Morphometric measurements are listed in Table 1.

All measurements and counts were taken from the left side (except for gill raker counts, gill raker length, and lower arch length, which were taken from the first gill arch on the right side), unless the area was damaged. Observations added to the sampling regime after the season commenced included: size of three largest spots below the lateral line (right side), number of spots (right side), axillary process length (left side), and mouth color.

Morphometric/Meristic Data Analysis

Groups for which morphometric and meristic data was generated and tested against were: 1) all Arctic char versus all Dolly Varden, 2) Dolly Varden from the Egegik River versus Dolly Varden from Ruth River, and 3) small "benthic form" Arctic char versus all other Arctic char within the same length distribution (230-450

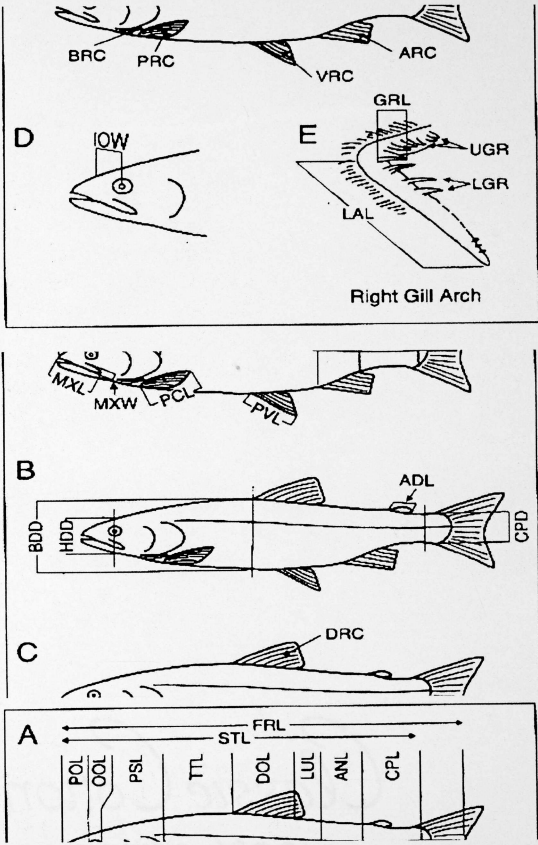


Figure 2. Morphometric and meristic variables measured for each fish. Variable acronyms explained on page 13 and in Table 1. Taken from Reist et al. (1995).

Table 1. Definitions of acronyms for morphometric measurements. Visual descriptions are given in Figure 2.

Acronym	Definition	Description
POL	preorbital length	from the tip of the snout to the anterior margin of the orbit
OOL	orbital length	from the anterior margin to the posterior margin of the orbit
PSL	postorbital length	from the posterior margin of the orbit to the posterior bony margin of the operculum
TTL	trunk length	from the posterior margin of the operculum to the origin of the dorsal fin
DOL	dorsal length	from the origin to the posterior insertion of the dorsal fin
LUL	lumbar length	from the posterior insertion of the dorsal fin to the origin of the anal fin
ANL	anal length	from the origin to the posterior insertion of the anal fin
CPL	caudal peduncle length	from the posterior insertion of the anal fin to the caudal flexure
HDD	head depth	distance centered at mid-pupil from top of head to the bottom of the jaw with the mouth closed
BDD	body depth	from the origin of the dorsal fin vertically to the belly without compression
CPD	caudal peduncle depth	the narrowest vertical distance along the peduncle
IOW	interorbital width	across the body axis between the bony margins of the orbits

Table 1. continued.

Acronym	Definition	Description
MXL	maxillary length	tip of snout to end of maxilla
MXW	maxillary width	widest measure across the maxilla
PCL	pectoral fin length	origin of the pectoral fin to the tip of the first ray
ADL	adipose length	origin of the fin to the tip of the longest ray
GRL	middle gill raker length	from the origin of the arch to the tip
LAL	lower arch length	from the base of the middle gill raker to the bottom of the lower gill arch

mm). The first test, all Arctic char versus all Dolly Varden, was done in order to confirm that both species do coexist in the same system and to determine if the very basic diagnostic cues commonly used in quick field identification of these two species is reliable. The second test, Egegik River Dolly Varden versus Ruth River Dolly Varden, was conducted because upon sampling these two groups of fish, it was evident that while they both appeared to be Dolly Varden, there were considerable differences in body condition, color, and overall shape. These two groups of fish were caught only several days apart and it is unlikely that these differences would have been related to seasonal changes in food availability or other environmental conditions. The third test, small "benthic form" Arctic char versus all other Arctic char (within the same length distribution as the benthic form) was conducted based upon differences in head morphology (the smaller benthic form had many large, sharp palatine and vomerine teeth, whereas the others did not) as well as location caught: the benthic form fish were all caught in one large basin of the lake (Island Arm), always in 25-50 m of water, and always on the bottom. All other Arctic char used in this test were caught in a variety of water depths and locations, including the Egegik River. The length distribution was truncated for both groups (260-450 mm) because this was the size range of benthic form fish caught (N=16). While isometric growth should reduce the effects of fish size on the data analysis for this test, I kept the length distribution of the normal form Arctic char tested (N=79) similar to make comparisons clearer between the two groups.

Morphometric and meristic data were analyzed using both univariate and multivariate statistical techniques. Three sets of data were generated for testing: meristics (counts), morphometrics (measurements) and residuals from the within-groups regression lines of morphometric data. The meristic data can be used directly in statistical analyses (the actual counts we recorded remain fixed throughout the fishes' post-larval life). The morphometric data must first be standardized to adjust for the size biases in the samples, and to dampen the effect of differences in the absolute sizes of body parts (Reist et al. 1995). This was done by calculating the ratio of the morphometric measurement to the standard length of the fish (tip of snout to the caudal flexure). However, ratio data is less mathematically correct than residual data (error terms can become compounded and correlations between variables used as the numerator may be inflated), therefore ratio data are used as an internal check for residual data only and are not reported (Reist 1985). Because salmonids experience isometric growth (body structures growing at equal rates) at a very young age (R. Smith, University of Alaska Fairbanks, personal communication), and only one sampled fish was less than 100 mm, an adjustment for allometric growth (body structures growing at different rates) was not deemed necessary. Analysis of covariance is used to generate the appropriate regression line for estimation of residuals (Reist et al. 1995).

To properly test the null hypothesis that measurements, counts, and residual values would have continuous distributions between groups tested, I had to choose a grouping criteria that was independent of the variables used in the analysis so as to

not introduce bias into the test (Reist et al. 1995). The six groups were definable according to the following criteria:

1. Arctic char – size of three largest spots below lateral line relative to pupil diameter (typically spots are larger), general body coloration (typically dark brownish to steel gray), lack of dark coloration on paired fins, and inside mouth color (typically all white).
2. Dolly Varden – size of three largest spots below lateral line relative to pupil diameter (typically pupil is larger), general body coloration (typically deep blue), darkly-colored paired fins with white edges, and inside mouth color (typically partially or totally bright green).
3. Egegik River Dolly Varden – location caught, plus criteria (2) above.
4. Ruth River Dolly Varden – location caught, plus criteria (2) above.
5. “Benthic form” Arctic char – presence of many large teeth on palate, vomer, and maxillary, plus criteria (1) above.
6. “Normal form” Arctic char – absence of large teeth on palate, vomer, and maxillary, plus criteria (1) above.

Univariate testing consisted of comparison of mean values using analysis of variance. Multivariate testing consisted of comparison of groups using principal components analysis, a factor analysis technique used to identify a relatively small number of factors that can be used to represent relationships among sets of interrelated variables, and discriminant analysis, where linear combinations of

independent, or predictor, variables are formed and serve as the basis for classifying individuals into groups (Norusis 1993).

Otolith Microchemistry

Both otoliths were collected at the same time the morphometric and meristic data were collected. All otoliths were aged using the break-and-burn method, similar to that described by Barber and McFarlane (1987), at the Alaska Department of Fish and Game Sport Fish Lab in Fairbanks, Alaska. The otoliths were ground to within the first annulus using 100 μ m grit and 30 μ m grit lapping paper attached to a Dremel tool. The otoliths were then burned with an alcohol flame, coated with mineral oil, and examined with reflected light.

To determine anadromous movement, we analyzed 43 otoliths using the scanning proton microprobe at the Physics Department at the University of Guelph in Ontario, Canada. We chose the otoliths to use by first stratifying the lake into four areas: Egegik River, the main lake, Island Arm basin, and Ruth Arm basin (Figure 1). A minimum length of 425 mm fork length was chosen, so as to reduce the chances of running a test of anadromy on juvenile fish. Twenty-three Arctic char and twenty Dolly Varden were chosen: five from each of the four areas (except for the Dolly Varden in the main lake, where we only had three specimens). Six juvenile fish were run (three of each species) in attempt to get a baseline lake signal for comparisons. One Arctic char otolith from Ruth Lake was run as well.

The otoliths were embedded in epoxy resin and a transverse cut was made through the area encompassed by the first annulus (core). Otoliths were then

prepared for SPM analysis by sequentially grinding with 240, 320, 400, and 600 grit silicon carbide, then polished with 5, 3, 1, and 0.3 μm aluminum oxide, and finally coated with carbon (Babaluk et al. 1997). These preparatory steps were conducted at the Freshwater Institute at the Department of Fisheries and Oceans-Canada and at the University of Manitoba in Winnipeg, and then sent to the University of Guelph for microprobe analysis.

With the SPM, distribution maps of trace elements were recorded by directing a beam of protons, produced by an electrostatic accelerator, onto an otolith and recording the emitted X-ray flux (Campbell et al. 1995). The proton beam energizes the elements on the otolith to emit X-rays that have wavelengths unique to each particular element, a technique called PIXE (*Proton Induced X-ray Emission*). The emitted X-rays are then analyzed using a silicon/lithium detector. The X-ray spectrum is used to identify the elements present in the area of the otolith being examined, and the amount of a particular element is measured by the height of the peak (as counts). The SPM is particularly good at detecting strontium, with detection limits of 1-2 ppm (Campbell et al. 1995).

Stomach Contents

Stomach content information was recorded at time of morphometric and meristic data collection, and is reported as percent frequency of occurrence. Fishes were usually keyed out to species (unless digestion had been advanced too far, whereas the fish remains were labeled "unidentified fish"). Invertebrates were normally keyed only to family. Tabular representation was generated for comparison

between all Dolly Varden and Arctic char, between Dolly Varden from two different locations, and between two potential morphotypes of Arctic char.

Results

Arctic char versus Dolly Varden Morphology

Meristics

The univariate test of the null hypothesis for equality of meristic counts between Arctic char and Dolly Varden shows significant differences in all characters except anal ray counts and ventral ray counts (Table 2). The most notable difference between the two species was pyloric caecae counts, with Arctic char exhibiting a mean value of 48 and Dolly Varden showing a mean of 27.

Principal component analysis of the meristic variables is reported as the four components that explain the most variance in the sample, in descending order (Table 2). Principal component one (PC 1) shows high positive loadings for pyloric caecae, lower gill rakers, and ventral ray counts, and a negative loading for dorsal ray counts and pectoral ray counts. This component accounted for 26.7% of the variance in the sample. Principal component two was characterized by high positive loadings for pectoral ray counts and dorsal ray counts, and negative loading for pyloric caecae counts (Table 2). This component accounted for 16.3% of the variance in the sample. Components three and four can be interpreted in similar fashion, and account for 14.4% and 11.3% of the variance, respectively (the fewer factors needed to explain the variation, generally the better true separation). In examining the bivariate plot of

Table 2. Meristic variation in Arctic char (AC) and Dolly Varden (DV). Variable acronyms are given on page 12. Standardized and unstandardized coefficients for the discriminant analysis (DA) and coefficients of principal components analysis (PCA) 1, 2, 3, and 4 are given. Significance of the test for difference in character means is designated as NS=non-significant ($P>0.05$) and $**=P<0.01$.

Variable	Mean		Univar. sign.	DA coefficients		PCA coefficients			
	AC	DV		Std.	Unstd.	1	2	3	4
DRC	10.6	11.1	**	-0.115	-0.169	-0.379	0.524	-0.135	0.281
ARC	9.5	9.5	NS	0.090	0.128	-0.126	0.332	0.740	0.352
PRC	12.5	13.1	**	-0.208	-0.223	-0.204	0.636	-0.442	-0.316
VRC	9.1	9.1	NS	-0.017	0.033	0.700	0.544	0.485	-0.555
BRC	11.4	11.1	**	-0.022	-0.033	0.468	0.311	-0.158	0.251
UGR	8.9	8.3	**	-0.069	-0.067	0.564	0.325	-0.323	0.404
LGR	13.9	12.4	**	0.408	-0.466	0.821	0.096	0.076	0.121
PYL	48.1	26.9	**	0.854	0.147	0.847	-0.089	0.131	0.062
Constant	--	--	--	--	-8.469	--	--	--	--
Eigenvalue	--	--	--	3.339	--	2.135	1.305	1.148	0.901
% of variance	--	--	--	100	--	26.7	16.3	14.4	11.3
Significance	--	--	--	**	--	--	--	--	--

PC 1 and PC 2 scores (Figure 3A), clear grouping is exhibited between the two species, and almost no overlap exists. Plots of PC3 and PC4 scores showed no apparent grouping, and were not reported.

Multivariate examination of the hypothesis of equality of the Arctic char and Dolly Varden group centroids using discriminant analysis indicated that the two groups were significantly different ($P < 0.01$, $df = 8$) prior to the extraction of the discriminant function equation. The best discriminating variables were pyloric caecae and lower gill raker counts (both positive values) contrasted with pectoral and dorsal ray counts (negative values) (standardized coefficients, Table 2). The eigenvalue (the ratio of the between-groups to within-groups sums of squares) is fairly large, suggesting a “good” function (Norusis 1993). A plot of the discriminant scores (using a discriminant equation from the unstandardized coefficients and constant from Table 2) indicates a clear bimodal distribution of scores with minimal overlap (Figure 4A). There is a clear tendency for Dolly Varden to score on the negative end of the axis (group centroid = -2.97) and the Arctic char to score on the positive end (group centroid = 1.11). Classification accuracy of predicted group membership was excellent (98.37% correct classification overall), with 97.8% of Arctic char and 100% of Dolly Varden classified correctly.

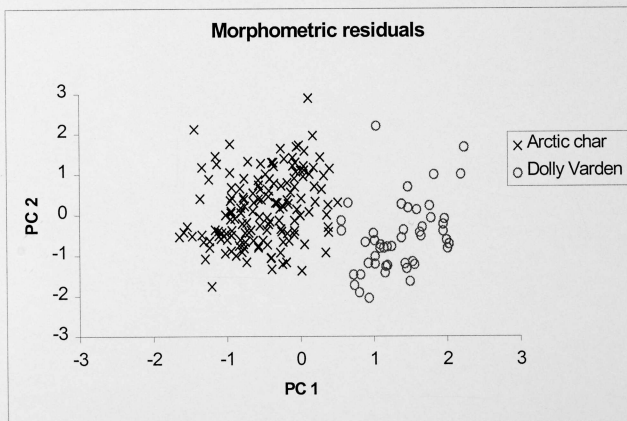
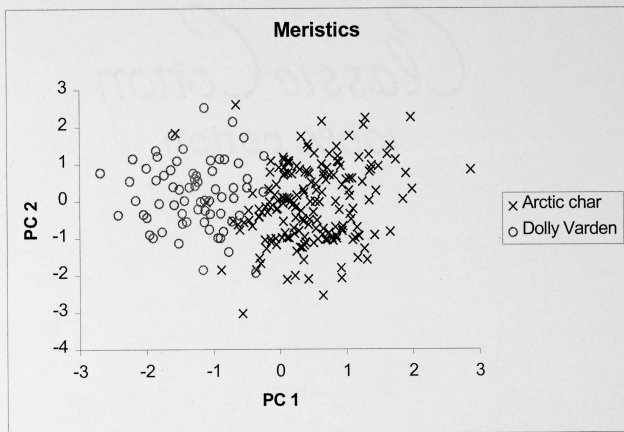


Figure 3. Plots of scores for the first two principal components for meristic (A) and residual morphometric (B) data from prior designated Arctic char and Dolly Varden.

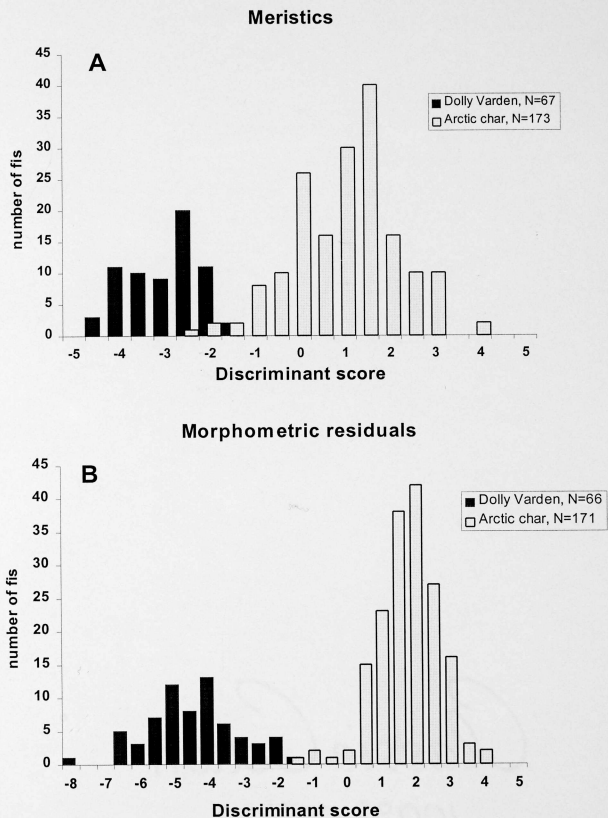


Figure 4. Histograms of meristic (A) and residual morphometric (B) discriminant scores for prior designated Arctic char and Dolly Varden.

Morphometry

The univariate test of the null hypothesis for continuous distribution of morphometric characteristics between Arctic char and Dolly Varden shows significant differences in 11 out of 17 characters, with particularly large differences in lumbar length, trunk length, and caudal peduncle depth (Table 3).

Principal component one shows high positive loadings for caudal peduncle depth, dorsal length, and anal length, and high negative loadings for orbital length and lumbar length. This component accounted for 27.5% of the variance in the sample. Principal component two was characterized by high positive loadings for maxillary length, preorbital length, head depth, and postorbital length (Table 3). This component accounted for 18% of the variance in the sample. Components three and four accounted for 8.9% and 6.0% of the variance, respectively. The bivariate plot of PC 1 and PC 2 scores show clear grouping of each species with no overlap (Figure 3B). Plots of PC 3 and PC 4 showed little apparent grouping, likely due to their weak contribution to the sample variance explanation (14.9% combined) in comparison to PC 1 and PC 2 (45% combined) and were not reported.

Multivariate examination of the hypothesis of equality of the Arctic char and Dolly Varden morphometric group centroids using discriminant analysis indicated that the groups were significantly different ($P < 0.01$, $df=17$) prior to the extraction of the discriminant function equation.

Table 3. Morphometric variation in Arctic char (AC) and Dolly Varden (DV). Variable acronyms are given in Table 1. Means are the least-square means estimate from the common-within-species regression lines of the variable against standard length. Standardized and unstandardized coefficients for the discriminant analysis (DA) and coefficients and principal components (PCA) 1, 2, 3, and 4 are given. Significance of the test for difference in character means is designated as NS=non-significant ($P>0.05$) and $**=P<0.01$.

Variable	Mean		Univa sign.	DA coefficients		PCA coefficients			
	AC	DV		Std.	Unstd.	1	2	3	4
POL	17.9	16.9	NS	-0.013	-0.004	0.138	0.704	-0.325	0.024
OOL	12.0	10.2	**	0.272	0.312	-0.766	0.338	0.104	0.096
PSL	44.3	44.5	NS	0.139	0.049	0.221	0.662	-0.103	0.385
TTL	97.5	91.6	**	0.242	0.429	-0.464	-0.241	0.560	-0.141
DOL	44.3	52.7	**	-0.404	-0.082	0.820	0.073	-0.006	-0.044
LUL	67.0	59.6	**	0.160	0.021	-0.700	-0.043	0.311	0.248
ANL	32.1	37.5	**	-0.198	-0.065	0.705	0.120	-0.140	-0.231
CPL	61.1	62.6	NS	-0.157	-0.244	0.301	-0.112	0.216	0.771
HDD	42.0	41.7	NS	0.073	0.017	0.219	0.686	0.068	-0.985
BDD	72.7	76.5	**	0.370	0.042	0.423	0.015	0.685	-0.190
CPD	24.7	31.8	**	-0.796	-0.364	0.901	0.016	0.111	-0.100
IOW	34.5	33.9	NS	-0.052	-0.019	0.045	0.637	0.425	-0.043
MXL	35.0	33.2	**	-0.044	-0.011	-0.065	0.718	-0.175	-0.250
MXW	6.7	5.8	**	0.335	0.341	-0.200	0.375	0.440	-0.119
PCL	53.6	54.8	NS	-0.045	-0.008	0.336	0.640	-0.013	0.116
LAL	33.6	28.9	**	0.671	0.272	-0.540	0.532	-0.137	0.104
GRL	4.6	6.2	**	-0.246	-0.223	0.598	-0.024	-0.101	0.139
Constant	--	--	--	--	-0.143	--	--	--	--
Eigenvalue	--	--	--	8.169	--	5.506	3.596	1.782	1.200
% of variance	--	--	--	100	--	27.5	18.0	8.9	6.0
Significance	--	--	--	**	--	--	--	--	--

The best discriminating variables were lower arch length and body depth (both positive values) contrasted with caudal peduncle depth and dorsal length (negative values) (standardized coefficients, Table 3). The eigenvalue is large (8.169), suggesting a good function. A plot of the discriminant scores indicates clear bimodality with minimal overlap (Figure 4B). The group centroid for Arctic char is 1.79, and for Dolly Varden, -4.53. Classification accuracy of predicted group membership is high (99.19% correct classification overall), with 99.4% of Arctic char and 98.6% of Dolly Varden classified correctly.

Egegik River Dolly Varden versus Ruth River Dolly Varden

Meristics

The univariate test of the null hypothesis for equality of meristic counts between Egegik River and Ruth River Dolly Varden shows a significant difference for pyloric caecae counts only (Table 4).

Principal component one shows high positive loadings for upper gill raker and pyloric caecae counts and negative loadings for pectoral ray and anal ray counts (Table 4). This component accounted for 25% of the variance in the sample. High positive loading for dorsal ray counts and negative loading for ventral ray counts characterize principal component two. This component accounted for 20% of the variance in the sample. Components three and four accounted for 14.1% and 12.6% of the sample variance, respectively. The bivariate plot of PC 1 and PC 2 scores shows little apparent grouping, with the Egegik River fish scoring somewhat higher for PC 2 scores (Figure 5A).

Table 4. Meristic variation in Dolly Varden from Egegik River (ER) and Ruth River (RR). Variable acronyms are given on page 12. Standardized and unstandardized coefficients for the discriminant analysis (DA) and coefficients of principal components analysis (PCA) 1, 2, 3, and 4 are given. Significance of the test for difference in character means is designated as NS=non-significant ($P>0.05$) and **= $P<0.01$.

Variable	<u>Mean</u>		<u>Univar.</u>	<u>DA coefficients</u>		<u>PCA coefficients</u>			
	ER	RR	sign.	Std.	Unstd.	1	2	3	4
DRC	11.1	11.1	NS	0.000	0.000	-0.065	0.806	-0.224	0.121
ARC	9.6	9.5	NS	0.000	0.000	-0.343	0.333	0.761	0.352
PRC	13.4	13.1	NS	0.000	0.000	-0.702	0.194	-0.090	0.261
VRC	9.3	9.0	NS	0.000	0.000	0.139	-0.807	0.099	0.373
BRC	11.0	11.2	NS	0.000	0.000	0.468	0.311	-0.158	0.251
UGR	8.4	7.9	NS	0.000	0.000	0.836	0.100	-0.042	0.276
LGR	12.2	12.1	NS	0.000	0.000	0.445	0.027	0.668	-0.017
PYL	27.8	23.6	**	1.000	0.274	0.527	0.420	-0.035	0.389
Constant	--	--	--	--	-7.018	--	--	--	--
Eigenvalue	--	--	--	0.350	--	2.000	1.600	1.126	1.004
% of variance	--	--	--	100	--	25.0	20.0	14.1	12.6
Significance	--	--	--	**	--	--	--	--	--

Table 5. Morphometric variation in Dolly Varden from Egegik River and Ruth River. Variable acronyms are given in Table 1. Means are the least-square means estimate from the common-within-species regression lines of the variable against standard length. Standardized and unstandardized coefficients for the Discriminant equation and coefficients of Principal Components 1, 2, 3, and 4 are given. Significance of the ANOVA test for difference in character means is designated as NS = non-significant ($P>0.05$) and ** = $P<0.01$.

Variable	Mean		Univar. sign.	DA coefficients		PCA coefficients			
	ER	RR		Std.	Unstd.	1	2	3	4
POL	19.3	19.9	NS	-0.785	-0.227	0.493	-0.601	-0.468	0.055
OOL	11.5	10.8	NS	-0.545	-0.530	0.500	-0.342	0.545	0.186
PSL	49.5	50.0	NS	0.326	0.158	0.517	-0.483	-0.329	-0.002
TTL	100.6	102.9	NS	-0.645	-0.163	0.046	0.805	0.277	0.067
DOL	63.8	57.0	**	-0.807	-0.222	-0.028	-0.702	0.439	-0.383
LUL	59.5	67.2	**	0.858	0.129	-0.128	0.704	-0.216	0.445
ANL	39.3	41.4	NS	0.521	0.190	0.560	0.249	-0.043	-0.466
CPL	58.6	73.5	**	1.014	0.216	0.602	0.489	-0.391	0.021
HDD	46.3	45.4	NS	-0.354	-0.118	0.295	-0.391	0.142	0.626
BDD	78.9	90.0	**	0.465	0.085	0.620	0.636	-0.013	0.082
CPD	33.9	36.9	**	0.397	0.123	0.569	0.491	0.234	0.059
IOW	39.1	41.4	NS	0.197	0.083	-0.121	-0.218	0.523	0.298
MXL	34.7	39.2	**	1.169	0.246	0.688	-0.313	-0.475	0.158
MXW	5.9	6.6	NS	-0.513	-0.409	0.694	0.237	0.279	-0.148
PCL	60.5	60.9	NS	-0.188	-0.041	0.576	-0.470	0.101	0.247
LAL	30.5	32.2	NS	0.703	0.238	0.819	-0.151	0.125	-0.050
GRL	6.0	6.6	NS	-0.323	-0.267	0.638	0.281	0.357	-0.072
Constant	--	--	--	--	-0.147	--	--	--	--
Eigenvalue	--	--	--	18.831	--	4.630	3.972	1.901	1.210
% of variance	--	--	--	100	--	27.2	23.4	11.2	7.1
Significance	--	--	--	**	--	--	--	--	--

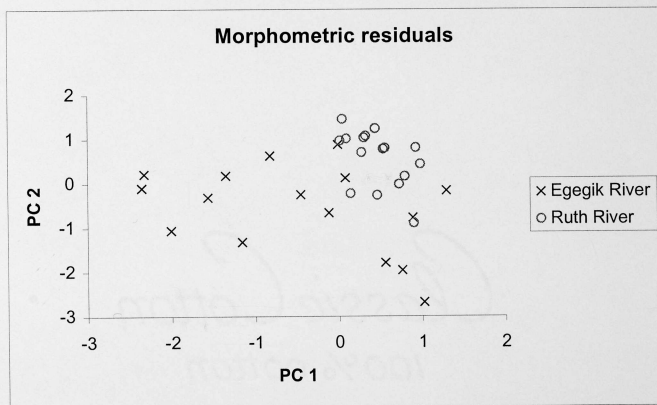
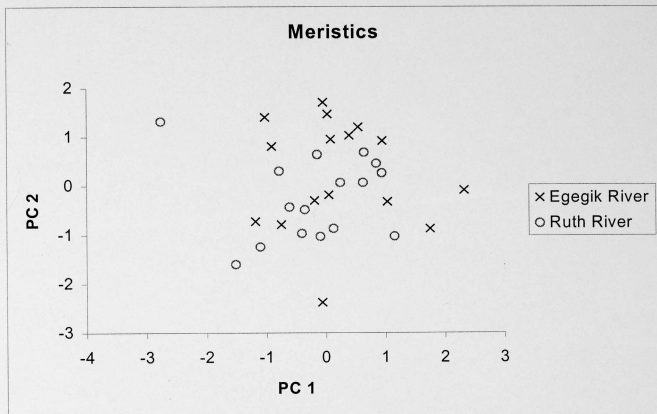


Figure 5. Plots of scores for the first two principal components for meristic (A) and residual morphometric (B) data from prior designated Dolly Varden.

Multivariate examination of the hypothesis of equality of Egegik River and Ruth River Dolly Varden group centroids using discriminant analysis indicates that the two groups were significantly different based upon pyloric caecae counts only ($P < 0.01$, $df = 1$) prior to the extraction of the discriminant function equation. Pyloric caecae counts was the only variable that contributed to the discriminant function equation (not including the constant) (Table 4). The eigenvalue is small (0.35), suggesting a weak function. A plot of the discriminant scores shows high overlap, but a clear trend for the Ruth River Dolly Varden to score lower (group centroid = -0.57) than the Egegik River Dolly Varden (group centroid = 0.57) (Figure 6A). Classification accuracy for predicted group membership was 68.8% overall, with 81.3% of Egegik River fish and 56.3 % of Ruth River fish classified correctly.

Morphometry

The univariate test of the null hypothesis for continuous distribution of morphometry between Egegik River and Ruth River Dolly Varden showed significant differences in six out of seventeen characters (Table 5). Particularly large differences in mean values were observed in body depth and caudal peduncle length.

Principal component one shows high positive loadings for lower arch length, maxillary width, and maxillary length. This component accounted for 27.2% of the variance in the sample. Principal component two shows high positive loadings for trunk length lumbar length, and negative loadings for dorsal length and preorbital length (Table 5). This component accounted for 23.4% of the sample.

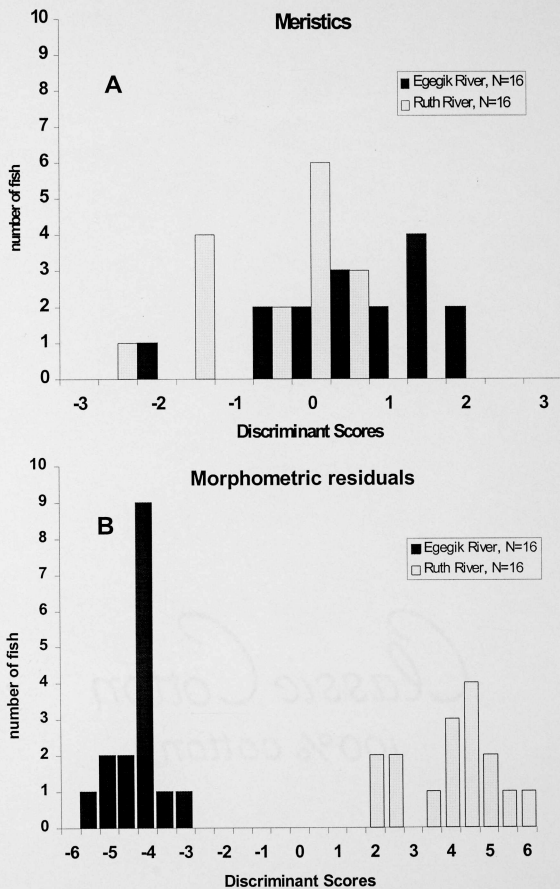


Figure 6. Histograms of meristic (A) and residual morphometric (B) discriminant scores for prior designated Dolly Varden.

Components three and four accounted for 11.2% and 7.1% of the variance, respectively. In examining the bivariate plot of PC 1 and PC 2 scores (Figure 5B), Egegik River fish showed a wide range of distribution with no apparent grouping, while the Ruth River fish showed clear grouping, with separation between the two groups much more apparent than in the meristic plots.

Multivariate examination of the hypothesis of equality of the Egegik River and Ruth River fish centroids using discriminant analysis indicated that the two groups were significantly different ($P < 0.01$, $N = 17$) prior to the extraction of the discriminant function equation. The best discriminating variables were maxillary length and lumbar length (both positive values) contrasted with dorsal length and preorbital length (both negative values) (standardized coefficients, Table 5). The eigenvalue is large (18.831), suggesting a good function. A plot of the discriminant scores (using a discriminant function equation from the unstandardized coefficients and constant from Table 5) indicates a clear bimodal distribution of scores with no overlap (Figure 6B). Classification accuracy of predicted group membership was perfect (100% correct classification into groups). The group centroid for Egegik River Dolly Varden is -4.20, and for Ruth River Dolly Varden, 4.20.

“Benthic Form” versus “Normal Form” Arctic char

Meristics

The univariate test of the null hypothesis for continuous distribution of meristic counts between benthic form and normal form Arctic char shows significant differences in only two out of the eight characters (anal ray counts and pectoral ray counts) (Table 6).

Principal component one showed moderate positive loadings for upper and lower gill raker counts and negative loading for ventral ray counts (Table 6). This component accounted for 19.2% of the variance in the sample. Principal component two showed high positive loadings for dorsal ray and branchiostegal ray counts. This component accounted for 17.7% of the variance in the sample. Components three and four accounted for 16.0% and 14.4% of the variance, respectively. The bivariate plot of PC 1 and PC 2 scores (Figure 7A) shows no apparent grouping.

Multivariate examination of the hypothesis of equality of the benthic form and normal form Arctic char group centroids using discriminant analysis indicated that the two groups were just short of being statistically different ($P=0.05$, $N=8$) prior to the extraction of the discriminant function equation. The best discriminating variables were pectoral ray counts (positive value) and anal ray counts (negative value) (standardized coefficients, Table 6).

Table 6. Meristic variation in benthic (BF) and normal form (NF) Arctic char. Variable acronyms are given on page 12. Standardized and unstandardized coefficients for the discriminant analysis (DA) and coefficients of principal components (PCA) 1, 2, 3, and 4 are given. Significance of the test for difference in character means is designated as NS=non-significant ($P>0.05$) and $**=P<0.01$.

Variable	Mean		Univar. sign.	DA coefficients		PCA coefficients			
	BF	NF		Std.	Unstd.	1	2	3	4
DRC	10.4	10.7	NS	0.433	0.556	-0.022	0.661	0.267	-0.322
ARC	9.9	9.4	**	-0.638	-0.881	-0.297	0.374	0.670	0.363
PRC	12.0	12.7	**	0.605	0.646	0.513	0.434	-0.302	-0.186
VRC	9.1	9.1	NS	0.137	0.033	-0.441	0.544	-0.254	-0.555
BRC	11.4	11.4	NS	-0.069	0.281	-0.183	0.635	-0.284	-0.442
UGR	8.5	8.7	NS	-0.084	-0.128	0.536	0.019	0.310	0.048
LGR	13.7	13.8	NS	0.135	0.165	0.556	-0.130	0.515	-0.150
PYL	45.5	48.0	NS	0.390	0.064	0.471	-0.229	-0.028	0.667
Constant	--	--	--	--	-11.386	--	--	--	--
Eigenvalue	--	--	--	0.244	--	1.344	1.237	1.122	1.005
% of variance	--	--	--	100	--	19.2	17.7	16.0	14.4
Significance	--	--	--	**	--	--	--	--	--

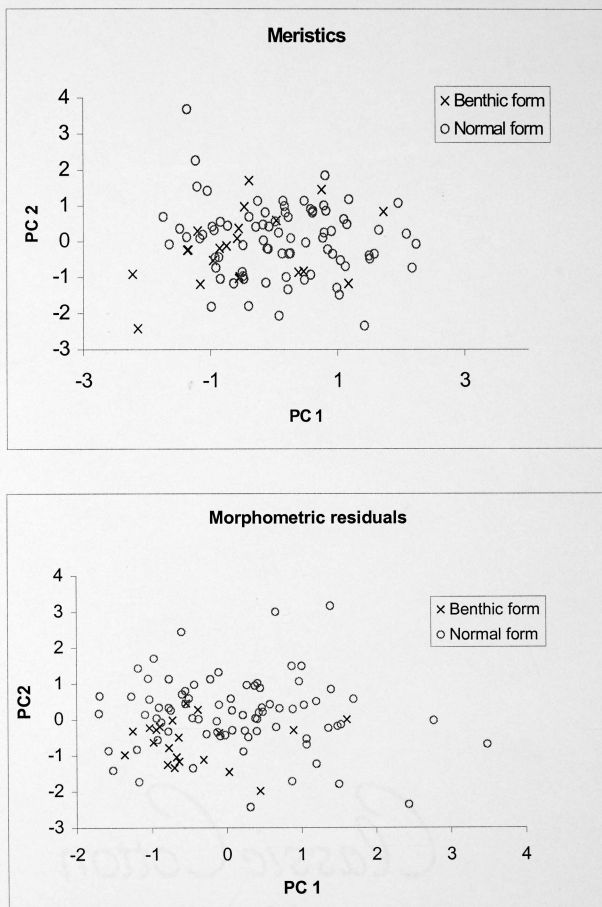


Figure 7. Plots of scores for the first two principal components for meristic (A) and residual morphometric (B) data from prior designated Arctic char forms.

The eigenvalue was small (0.244) suggesting a weak function. The plot of the discriminant scores indicates moderate overlap but a clear trend for the benthic form to score lower (Figure 8A). The group centroid for benthic form Arctic char was -0.949, and 0.252 for normal form Arctic char. Classification accuracy was good for overall predicted group membership (82.0%), but this may be artificially high due to the disparity in sample size. The benthic form (N=21) showed 66.7% misclassification, whereas the normal form (N=79) showed only 3.8% misclassification, suggesting that 90% of all fish should be classified as normal form Arctic char.

Morphometry

The univariate test of the null hypothesis for continuous distribution of morphometric variation between benthic form and normal form Arctic char shows significant differences in five out of seventeen characters, with body depth showing the largest differences in mean values (Table 7). Principal component one was characterized by high positive loadings for head depth and postorbital length, and negative loading for lumbar length. This component accounted for 20.5% of the variance in the sample. Principal component two showed high positive loading for body depth and negative loading for anal length. This component accounted for 12.7% of the variance in the sample.

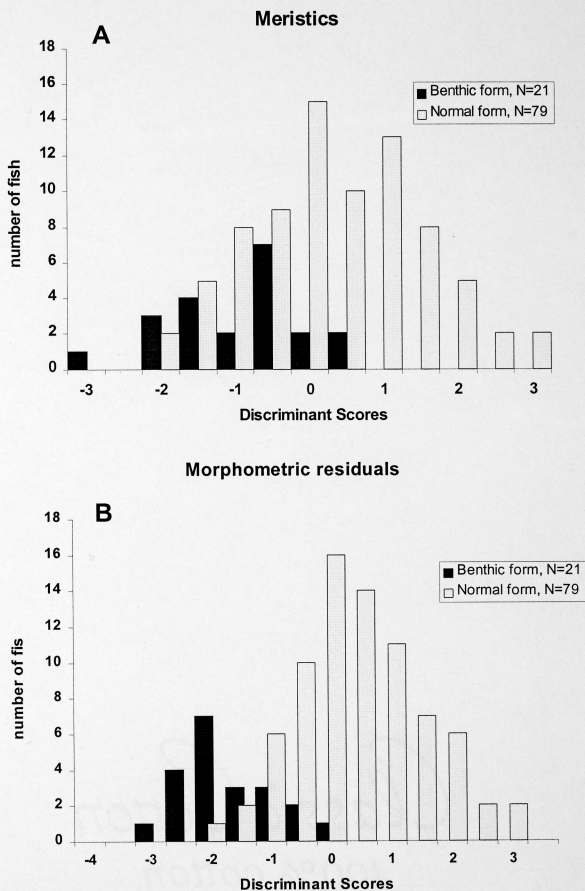


Figure 8. Histograms of meristic (A) and residual morphometric (B) discriminant scores for prior designated Arctic char forms.

Table 7. Morphometric variation in benthic and normal form Arctic char. Variable acronyms are given in Table 1. Means are the least-square means estimate from the common-within-species regression lines of the variable against standard length. Standardized and unstandardized coefficients for the Discriminant (DA) and coefficients and principal components analysis (PCA) coefficients 1, 2, 3, and 4 are given. Significance of the test for difference in character means is designated as NS=non-significant ($P>0.05$) and $**=P<0.01$.

Variable	Mean		Univar. sign.	DA coefficients		PCA coefficients			
	BF	NF		Std.	Unstd.	1	2	3	4
POL	15.5	15.6	NS	-0.086	-0.041	0.543	-0.262	-0.411	0.007
OOL	11.8	11.4	NS	-0.623	-0.726	0.362	0.209	-0.192	0.228
PSL	39.3	40.5	NS	0.148	0.060	0.670	-0.054	0.368	0.066
TTL	89.7	88.8	NS	0.135	0.012	-0.227	0.032	-0.075	0.598
DOL	38.4	40.0	NS	0.056	0.020	0.206	0.095	0.382	-0.042
LUL	63.2	64.2	NS	0.489	0.130	-0.392	0.110	-0.324	0.311
ANL	29.1	29.5	NS	0.389	0.157	0.273	-0.474	0.175	0.204
CPL	56.1	58.4	**	0.341	0.096	-0.064	0.322	0.588	-0.322
HDD	35.2	38.0	**	0.486	0.142	0.801	0.146	-0.213	-0.128
BDD	61.0	66.4	**	0.074	0.011	0.214	0.716	0.005	0.207
CPD	21.6	22.7	**	0.211	0.159	0.342	0.548	0.361	0.305
IOW	29.2	31.7	**	0.487	0.190	0.636	0.376	-0.107	-0.013
MXL	32.4	32.0	NS	-0.388	-0.011	0.593	-0.372	-0.326	-0.198
MXW	5.7	6.2	NS	0.329	0.339	0.282	0.459	-0.524	-0.281
PCL	45.7	47.9	NS	0.228	0.041	0.639	-0.138	0.275	0.003
LAL	30.4	30.4	NS	-0.126	-0.068	0.482	-0.520	0.214	0.365
GRL	4.4	4.4	NS	-0.015	-0.022	0.068	0.092	-0.158	0.365
Constant	--	--	--	--	0.057	--	--	--	--
Eigenvalue	--	--	--	0.794	--	3.487	2.156	1.690	1.402
% of variance	--	--	--	100	--	20.5	12.7	9.9	8.2
Significance	--	--	--	**	--	--	--	--	--

Components three and four accounted for 9.9% and 8.2% of the variance, respectively (Table 7). In examining the bivariate plot of PC 1 and PC 2 scores (Figure 7B) little evidence of grouping exists, but there is a definite trend for the benthic form char to exhibit a lower PC 2 score than the normal form fish.

Multivariate examination of the hypothesis of equality of benthic form and normal form group centroids using discriminant analysis indicated that the two groups were significantly different ($P < 0.01$, $df = 17$) prior to the extraction of the discriminant function equation. The eigenvalue (the ratio of the between-groups to within-groups sums of squares) is 0.794, suggesting a moderately good function (Table 7). A plot of the discriminant scores (Figure 8B) shows a trend for the benthic form fish (group centroid = -1.71) to score lower than the normal form (group centroid = 0.45), with only one fish scoring greater than zero. Classification accuracy was good, with 71.4% of benthic form fish correctly classified, and 96.2% of normal form fish correctly classified (91% correct classification overall).

Otolith Microchemistry

Water Sample Analysis

Water samples for strontium concentration were taken during summers 1996 (for lake samples) and 1997 (for inlet streams and outlet river samples). Four stations within Becharof Lake were sampled, with strontium concentrations ranging from 0.14 ppm to 0.26 ppm (LaPerriere 1998). Streams large enough for Dolly Varden to inhabit (about 11 inlet streams plus the outlet river) showed strontium concentrations ranging from 0.10 ppm to 0.29 ppm (LaPerriere 1999). Using a regression function

developed by Babaluk and Reist (unpublished data) predicting the relationship between strontium in the otolith core and the strontium in the water, the predicted otolith strontium concentration in these fish would be 300-500 ppm for a Becharof Lake signal and 150-650 ppm for stream signals. We did not have a seawater water sample, but strontium concentrations in otoliths of known anadromous Arctic char from four locations in the Canadian Arctic have anadromy signals of 1500-2000 ppm Babaluk et al. (1997). We will assume a similar relationship exists here in lieu of water data.

Arctic Char Line Scan Data

Twenty-seven Arctic char otoliths were run from fish ages 3-13 years. Twelve fish exhibited what we believe to be a strictly freshwater signal (250-500 ppm) such as in Figure 9 and Appendix Figure A5. Some of these fish showed slight rises up to 650 ppm, which may be attributed to feeding around a stream outlet of a higher signal or ascending a stream to feed. These fish ranged in age from 3-11 years, and included at least three spawners and all three "benthic form" fish tested. Line scans from all twelve of these fish are shown in Appendix A.

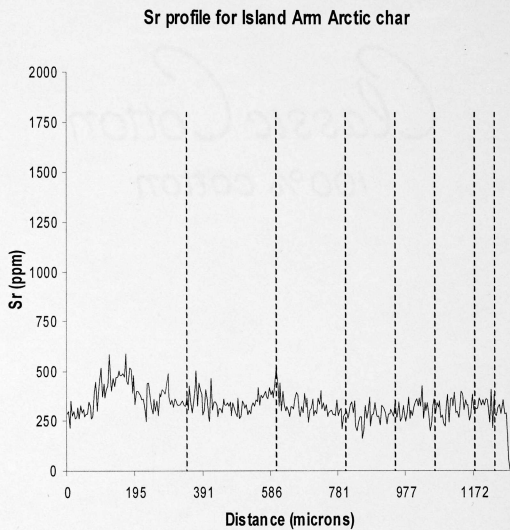


Figure 9. Strontium line scan from a non-anadromous Arctic char (dashed lines denote annuli).

Five fish exhibited what appear to be full anadromy signals (1500-2000 ppm) in addition to freshwater signals such as in Figure 10 and Appendix Figure B2. Some of these fish showed consistent strontium concentrations of 700-900 ppm for over two years, suggesting residence in a water body other than the Becharof drainage. Anadromous movement appeared to begin between ages 2-8, and did not always occur in consecutive years. These fish ranged in age from 6-12 years, and one fish appeared to have a healed lamprey scar. Line scans from all five of these fish are shown in Appendix B.

Six fish exhibited signals that were difficult to interpret as strict freshwater residence or anadromous movement, such as in Figure 11 and Appendix Figure C3. These fish ranged in age from 7-13 years. Four fish exhibited an "intermediate" signal (700-900 ppm) from the primordium (age < 1 year) through the first 1-3 annuli, suggesting residence somewhere other than the Becharof drainage. These fish appeared to show movement to and from water of higher and lower salinity (Sr up to 1600 ppm, but generally 1200 ppm or less), but without movement to true saltwater as witnessed in the anadromous fish. Two fish exhibited an apparent freshwater signal for the first 2-3 years, then showed an extended period of intermediate freshwater/saltwater signals. Line scans from all six of these fish are shown in Appendix C.

Sr profile from Egegik River Arctic char

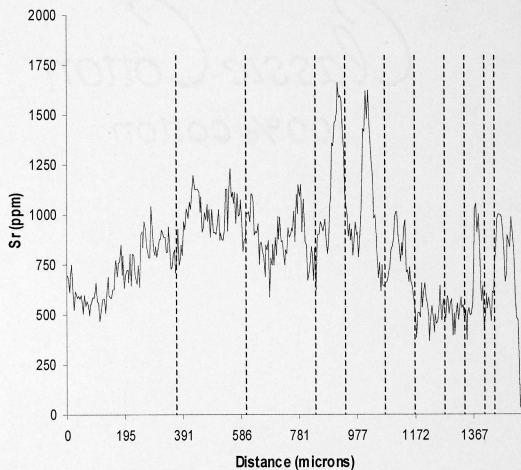


Figure 10. Strontium line scan from an anadromous Arctic char (dashed lines denote annuli).

Sr profile from main lake Arctic char

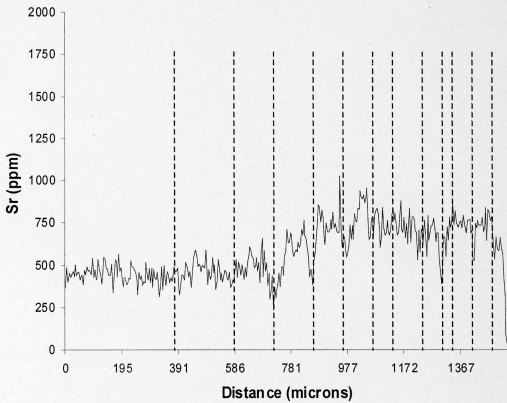


Figure 11. Strontium line scan from an Arctic char that is difficult to interpret with respect to anadromy (dashed lines denote annuli).

Dolly Varden Line Scan Data

Twenty Dolly Varden otoliths were run, ranging in ages from 3-12 years, and including at least one spawner. Seven fish exhibited what appears to be a strictly freshwater strontium signal such as in Figure 12 and Appendix Figure D5, ranging from 400-700 ppm. These signals are consistent with what we would expect from the inlet streams, and may reflect between-stream movement. Two of these fish were caught in the Egegik River near the lake outlet. One fish was captured, marked (Floy tag), in Gertrude Creek (a tributary of the King Salmon River) by the Fish and Wildlife Service and recaptured in Cleo Creek. This reflects movement down the King Salmon River to the Egegik River inlet (where it certainly encountered brackish water briefly), up the Egegik and across the lake and into Island Arm, a distance of over 150km. The highest peak, 600 ppm strontium, was recorded when the fish was five years old and may reflect the time at which this movement was undertaken. Another fish was also tagged in Gertrude Creek, and showed a peak strontium concentration of 750 ppm. One fish captured in Bible Creek had what appeared to be a lamprey scar, yet its highest recorded strontium concentration was only 600 ppm. Line scans from all seven of these fish are shown in Appendix D.

Two fish exhibited what appears to be true anadromy signals, with peaks as high as 2500 ppm Sr such as in Figure 13 and Appendix Figure E 2. These fish were

Sr profile from Bible Creek Dolly Varden

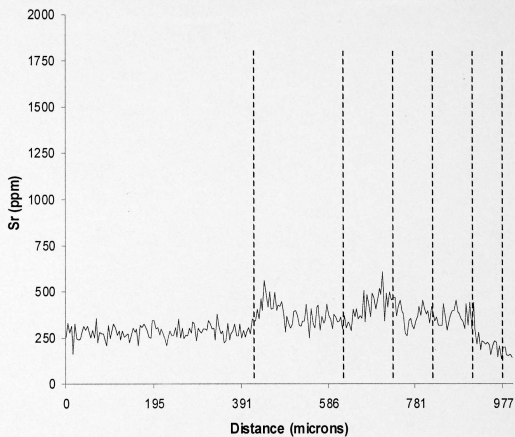


Figure 12. Strontium line scan from a non-anadromous Dolly Varden (dashed lines denote annuli).

Sr profile from Egegik River Dolly Varden

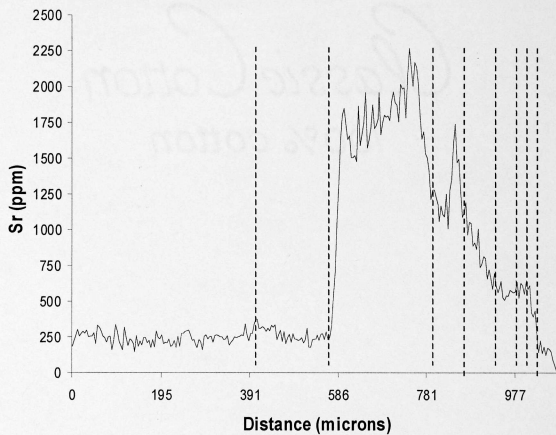


Figure 13. Strontium line scan from an anadromous Dolly Varden (dashed lines denote annuli).

caught in the Egegik River in late May, and show almost identical signals throughout the scans, but were five and eight years old, respectively. The line scans from these fish are shown in Appendix E.

Eleven fish exhibited signals that were difficult to interpret with respect to anadromy with peaks up to 1000 ppm, such as in Figure 14 and Appendix Figure F9. These fish ranged in age from 4-9 years, and included all seven Ruth River Dolly Varden tested. Most of these fish showed obvious peaks and valleys, suggesting seasonal movement to different streams and possibly brief excursions to marine waters. Included in this group are one female spawner and a fish with what appears to be a lamprey scar. Line scans from all eleven of these fish are shown in Appendix F.

Stomach Contents

Arctic char versus Dolly Varden

A total of 16 different prey types were observed between the two species, plus many empty stomachs (Table 8). Isopods dominated the stomach contents of Arctic char (24% of fish stomachs sampled), followed by demersal fishes (nine-spined stickleback and pygmy whitefish) at a combined 16.5%. Fish observed inhabiting the nearshore environment (three-spined stickleback, slimy sculpin, and juvenile coho salmon) were recorded in 6.5% of sampled Arctic char stomachs. Unidentifiable fish (due to digestion processes) were observed in 16.7% of stomachs, but based on location caught and trends of other fish in the same catch, I believe that they are

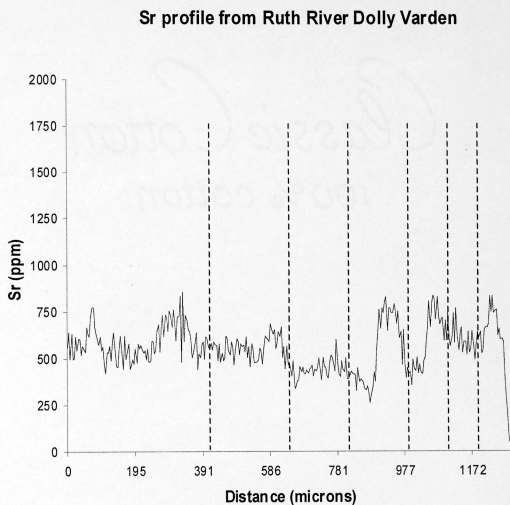


Figure 14. Strontium line scan from a Dolly Varden that is difficult to interpret with respect to anadromy (dashed lines denote annuli).

Table 8. Stomach contents of all Becharof Drainage Arctic char and Dolly Varden captured from 19 May 1998 through 15 September 1998. Values are given as number of observations and frequency of occurrence.

Item	Arctic char (N=200)	Dolly Varden (N=80)
Isopods	49 (24.1%)	7 (9.6%)
Nine-spined stickleback	26 (12.8%)	0 (0.0%)
Three-spined stickleback	9 (4.4%)	0 (0.0%)
Pygmy whitefish	7 (3.4%)	0 (0.0%)
Sockeye juveniles	6 (3.0%)	0 (0.0%)
Coho juveniles	2 (1.0%)	0 (0.0%)
Sculpin	2 (1.0%)	0 (0.0%)
Unidentified fish	34 (16.7%)	2 (2.4%)
Sockeye eggs	3 (1.5%)	15 (18.5%)
Unknown eggs	1 (0.5%)	3 (3.7%)
Dipterans	12 (5.9%)	12 (14.8%)
Trichopterans	3 (1.5%)	10 (12.3%)
Coleopterans	0 (0.0%)	6 (7.4%)
Unknown insects	0 (0.0%)	4 (4.9%)
Snails	5 (2.5%)	0 (0.0%)
Small mollusks	0 (0.0%)	1 (1.2%)
Empty stomachs	41 (20.2%)	20 (24.7%)

likely mostly nine-spined stickleback and pygmy whitefish. Pupae and emergent dipterans were observed in 5.9% of stomachs, probably captured as they made the vertical migration through the water column to the surface. Sockeye juveniles and eggs were a surprisingly low proportion of the diet of the Arctic char, accounting for 3.0% and 1.5% of observations, respectively (Table 8).

Dolly Varden exhibited a much smaller range of observed food types (Table 8). Invertebrate drift (trichopterans, dipterans, and coleopterans) accounted for the largest proportion of observed food types (46.3%). Sockeye eggs accounted for 18.5% of observed prey, and were the only food item observed in Dolly Varden stomachs after the sockeye salmon returned to spawn in inlet streams (mid-July through September). Isopods accounted for 9.6% of observed prey items and all but one of these observations were made from Dolly Varden captured in the Egegik River. Fish accounted for 2.4% of observed prey (recorded two times), and were too digested to identify to species.

Egegik River Dolly Varden versus Ruth River Dolly Varden

Sixty percent of Egegik River Dolly Varden stomachs contained invertebrate drift (Diptera pupae-50% and Coleoptera-10%), and 30% contained isopods (Table 9). One fish stomach contained small gray eggs (1-2mm), possibly from an Arctic grayling (*Thymallus arcticus*) or a sculpin (*Cottus spp.*). Fish were not observed as a prey item.

The Ruth River Dolly Varden stomachs usually contained either invertebrate drift in the form of dipterans, coleopterans, or other insects (47.1%) or nothing at all

Table 9. Stomach contents of Egegik River Dolly Varden and Ruth River Dolly Varden captured from 19 May 1998 through 9 June 1998. Values are given as number of observations and frequency of occurrence.

Item	Egegik River (N=20)	Ruth River (N=17)
Dipterans	10 (50.0%)	2 (11.8%)
Isopods	6 (30.0%)	0 (0.0%)
Coleopterans	2 (10.0%)	0 (0.0%)
Trichopterans	0 (0.0%)	3 (17.6%)
Unidentified insects	0 (0.0%)	3 (17.6%)
Unidentified eggs	1 (5.0%)	0 (0.0%)
Small mollusks	0 (0.0%)	1 (5.9%)
Empty stomachs	1 (5.0%)	8 (47.1%)

(47.1%) (Table 9). One fish had a small mollusk in its stomach, possibly eaten incidentally during ingestion of an aquatic insect from the substrate. It is important to note that both the Egegik River and Ruth River fish were sampled 7-8 weeks before the return of the sockeye salmon, therefore salmon eggs could not be a potential food item at this time.

"Benthic form" Arctic char versus "Normal form" Arctic char

Stomachs of benthic form Arctic char contained mostly fish (52.3%) (Table 10). The demersal fishes, pygmy whitefish and nine-spined stickleback, were the most frequently observed (38%). Isopods were only observed in two stomachs (9.5%). Eight stomachs were empty (38.1%).

Normal form Arctic char exhibited a much wider range of food choices, with isopods recorded most often (21.2% of the time) (Table 10). Diptera larvae and emergents were recorded 11 times, and only one sockeye salmon was recorded.

Discussion

Dolly Varden and Arctic char

Morphometric analysis alone clearly separates Dolly Varden from Arctic char (e.g., bimodality in discriminant morphometry scores, excellent classification accuracy, etc.) as two physically distinct groups (Tables 2 and 3). This quantitative separation is further supported by observations of overall body shape and color, preferred habitats, and food types. Dolly Varden were captured almost exclusively in running waters (i.e., the inlet streams or the outlet river) and aside from 17 specimens

Table 10. Stomach contents of “benthic form” and “normal form” Arctic char collected from 6 June 1998 through 13 September 1998. Values are reported as number of observations and frequency of occurrence.

Item	Benthic form (N=21)	Normal form (N=85)
Pygmy whitefish	4 (19.0%)	4 (4.7%)
Nine-spined stickleback	4 (19.0%)	13 (15.3%)
Three-spined stickleback	1 (4.8%)	3 (3.5%)
Unidentified fish	2 (9.5%)	13 (15.3%)
Isopods	2 (9.5%)	18 (21.2%)
Dipterans	0 (0.0%)	11 (12.9%)
Snails	0 (0.0%)	3 (3.5%)
Trichopterans	0 (0.0%)	2 (2.4%)
Sockeye juveniles	0 (0.0%)	1 (1.2%)
Sculpin	0 (0.0%)	1 (1.2%)
Empty stomachs	8 (38.1%)	16 (18.8%)

collected from the Egegik River in early summer, all Arctic char were caught in the lake (N=162; see Appendix Tables A and B). It appears that the two species had no direct competition with each other during the summer months, at least in freshwater. I suspect that this habitat separation also precludes these two species from hybridizing at more than a nominal level. Neither species was observed spawning during the field season, and likely do not spawn until at least October. However, observations of body condition (coloration, kype formation, etc.) suggested that the Dolly Varden were much closer to spawning time than were the Arctic char when we left the study site (September 12).

Arctic char

The otolith microchemistry results reflect much overlap in movement patterns (Appendix Figures A-C). This is apparently the first direct evidence of anadromy in Arctic char in the state of Alaska (F. DeCicco, Alaska Department of Fish and Game, Fairbanks, personal communication). It was previously thought that anadromy in Arctic char generally increases with latitude, with the ultimate cause for this behavior tied to decreased productivity in fresh waters of northern systems (Nordeng 1983). Becharof Lake is near the southern latitudinal range limit for Arctic char in North America, therefore this observation was unexpected. The mechanism for anadromy in Arctic char this far south may not be based on lack of productivity in freshwater, but perhaps competition with the many other fishes that utilize similar resources. The four species of whitefishes found in the lake all utilize zooplankton for at least some portion of their lives, and observations of stomach contents of adult round, pygmy,

and lake whitefish all showed some dietary overlap with the Arctic char (particularly snails and isopods). Whitefishes may outcompete the Arctic char in some European lake systems (F. DeCicco, Alaska Department of Fish and Game, Fairbanks, personal communication), therefore anadromy may represent a mechanism to relieve inter-specific stress in freshwaters.

The ambiguous signals observed (up to 1000 ppm Sr; Appendix Figure C) are more difficult to interpret in terms of movement, but may reflect movement to estuarine environments. Estuaries provide abundant food and shelter for smaller fishes and juveniles (Diana 1995), and therefore may be an ideal environment for Arctic char--plenty of food, and avoidance of an extensive offshore migration. The eastern section of Bristol Bay receives freshwater inputs from numerous large rivers (including the Kvichak, Naknek, Egegik, Ugashik, and Nushagak Rivers), and may contribute to the intermediate strontium concentrations found in nearshore environments. The sustained intermediate anadromy signal has not been reported in the literature for chars before and remains open to interpretation, but has been observed for whitefishes in the Mackenzie River and interpreted in a similar fashion (J. Reist, Department of Fisheries and Oceans, Winnipeg, personal communication). Another interpretation of the intermediate signals may be that these fish spend extended periods of time in the Egegik River, which is tidal for most of its length. The diel fluctuations in salinity (and therefore strontium) concentrations of the water would seem to pose significant osmotic stress, and could be the cause of the ambiguous strontium signals..

The stomach contents of the Arctic char reflect a population with a broad feeding niche, but with smaller individual niches. Of the 173 fish sampled, only 27 had more than one type of food item in their stomachs. Of the 13 food types observed in Arctic char stomachs, only four may be considered ephemeral (sockeye eggs, unknown eggs, dipterans, and trichopterans), and these account for only 10.9% of observations (Table 8). Therefore, seasonal availability of food types may not be a factor. Sockeye salmon juveniles, perhaps the most abundant fish in the lake (juvenile outmigration in 1998: 70 million smolts) were only observed as a food item six times.

The Dolly Varden in the Becharof drainage appears to be the classic northern form based on meristic counts for gill rakers and pyloric caecae (Table 2) as defined by DeCicco (1989). As is common with Dolly Varden, the Becharof drainage fish exhibited an extensive range of movement over salinity gradients, and likely frequent other Bristol Bay drainages. Two tagged fish from the King Salmon River, and found in the Becharof drainage, moved over 200 km in just one year. It is unlikely that the Dolly Varden in the Becharof drainage (or any other Bristol Bay drainage, for that matter) can be considered to be a part of a closed population.

The stomach contents of the Dolly Varden suggest seasonal shifts in preference. While no sockeye salmon were observed in examined stomachs (Table 8), it is likely that they can feed heavily on smolts during the short spring outmigration (our sampling times did not correspond with this outmigration, but previous observations at the Alaska Department of Fish and Game smolt counting

station support this behavior). After the smolts have moved out, Dolly Varden appear to feed on invertebrate drift until the spawning sockeye salmon return. At this time only eggs were observed in stomachs, and invertebrate drift appeared to be ignored. Digging up of salmon redds by Dolly Varden was not observed, only feeding on eggs in drift or from the substrate. These eggs would likely not have hatched anyway, therefore feeding of this type would not constitute a predation pressure.

Quantitative separation of Arctic char and Dolly Varden as distinct species can be useful in various ways. First, these two fish are notoriously difficult to identify in the field, and having several bases for separation (not only appearance but also food preferences and habitats) can aid in identification. Second, while these two species in this particular are clearly distinct in many ways, they are managed in Alaska sportfisheries collectively as *chars*. This can be of particular interest in the Becharof drainage, for all observed sportfishing effort (as minimal as it was) was on the inlet streams and outlet river, and therefore almost completely focused (inadvertently, to be sure) on the Dolly Varden. Understanding the differences in life history strategies may help managers better understand how sportfish harvest may or may not affect these two species.

Egegik River and Ruth River Dolly Varden

The quantitative separation between these two groups is not as good as in the separation of Arctic char and Dolly Varden. Meristically there is almost no separation (Table 4), but this is not unexpected. Power (1997) reports that fish in

polar and more temperate waters tend to have more vertebrae and other meristic parts with increasing latitude. This is possibly due in part because fish may need more muscle to swim in the colder; more viscous water, and consequently need more of these structures for greater muscle attachment. The two groups were classified as nearly significantly different in the meristics test based on variation in pyloric caeca counts alone, but the effects of a small sample size may have influenced this result (N=16 for both).

Morphologically (using residual values from the within-groups regression line) the two groups show a much better separation (Table 5). The fish for each group were caught only 10 days apart, so any potential seasonal growth should not have influenced the data substantially. These two groups were chosen to test because of radical differences in appearance as well as location. The Egegik River fish had a silvery-bright coloration with faint spots (as one would expect from an anadromous fish fresh from the sea), whereas the Ruth River fish were a deep blue with bright pink spots. The Egegik River fish also appeared to be in poor condition, with several fish appearing emaciated. The Ruth River fish appeared much healthier and robust. Both the Egegik River and Ruth River serve as outlets for lakes; perhaps these locations could act as good locations as feeding stations for smolt outmigrations, and may serve as the basis for development of loosely-knit sub-populations.

Otolith microchemistry analysis shows that all tested Ruth River fish showed what appears to be a mild, possibly estuarine, movement signal, similar to the one found in the tagged fish from the King Salmon River. The Egegik River fish

exhibited signals of both mild anadromy and true oceanic movements. It seems likely that Dolly Varden throughout the Bristol Bay area congregate in outlet rivers of sockeye salmon nursery lakes in the spring, and these fish may have come from other systems to the Egegik to capitalize on the smolt outmigration. I suspect that while the Ruth River and Egegik River fish are not two discrete sub-populations, the Ruth River Dolly Varden probably exhibit less variability in stock structure, movement, and habits than do the Dolly Varden found in the Egegik River, even in the absence of any physical barrier besides distance between the two groups.

“BenthicForm” versus “Normal Form” Arctic char

Meristically, these two groups do not separate well (Table 6), and any apparent separation based on meristics may be influenced by disparity in sample size (benthic form: N=21; normal form: N=79). It is likely that the two groups would show continuous distributions if the benthic form sample size were larger.

Morphometrically, separation is much more apparent (Table 7). Much of the separation can be attributed to differences in head morphology, which was the most obvious difference in the field. This may be associated with feeding strategies; the benthic form showed a much narrower range of food preferences than did the normal form, with particular emphasis on the demersal fishes (nine-spined stickleback and pygmy whitefish). While the benthic form was often caught in the presence of large numbers of isopods, only twice were these fish found to have fed on them.

In the otolith microchemistry analyses, all three benthic form Arctic char tested showed a clear, strictly freshwater signal. The normal form fish showed a mix

of freshwater residency, mild anadromy, and true oceanic strontium signals. These results would support the notion of a benthic specialist, for a smaller range of movement would be consistent with a group of fish that focuses on a prey type found in a particular area, whereas as the more generalist group (the normal form fish) might show a wider range of movement patterns. All benthic form fish were caught in the Island Arm basin of the lake, and always in bottom sets in water 25-50m deep. The normal form fish were caught in a wide variety of areas, including shallow and deep water sets, and the outlet river.

Saavaitova (1990) reports that in nearly all populations of Arctic char, intermediate phenotypes are present and that it is often difficult to determine the status of distinct groups. While it appears that there may be more than one "form" of Arctic char in Becharof Lake, the differences in morphology and life history are not as obvious as those found in the chars of Lake Thingvallavatn in Iceland (Sandlund et al. 1992) and Lake El'gygytgyn in Russia (Cheresenev and Skopets 1990). This is likely due to differences in biological processes and age of these systems. Lake Thingvallavatn is about the same age as Becharof (both appear to have been glaciated during the Pleistocene) and is chemically similar, but Becharof Lake has at least 13 species of fish whereas Thingvallavatn has only three. Becharof Lake also has an outlet to sea (allowing movement in and out for anadromous fishes) while Thingvallavatn does not. These differences suggest that the char in Thingvallavatn have fewer options in terms of potential prey types and movement possibilities, competition for resources may be stronger, and therefore the specialization pressures

may be more intense. While Lake El'gygytgyn does have an outlet to the sea accessible to fishes, it is a much older system, probably formed as an impact crater from a meteor several million years ago, and was not glaciated (F. DeCicco, Alaska Department of Fish and Game, Fairbanks, personal communication). The chars of El'gygytgyn have had a much longer time to develop different forms than has Becharof Lake.

It appears that within both the Arctic char and Dolly Varden of the Becharof drainage, there are central tendencies in each species but with atypical individuals or even groups of fish. Both species have very plastic niches, and may even move to a different environment if need arises. The central tendency for Arctic char appears to be freshwater residency, with partial and full anadromy occurring less frequently. Environmental conditions within the lake seem favorable for strict residency, but perhaps inter- and intra-specific competition can trigger anadromy in times of resource stress. For Dolly Varden, the central tendency seems to be partial anadromy, with freshwater residence and full anadromy less common. Such fish may go into dilute seawater (estuaries or nearshore habitats receiving freshwater inputs) to feed or simply migrate through nearshore marine waters to other freshwaters, such as what was observed with the two fish tagged in the King Salmon River.

For future research, I would recommend tagging fish of both species, particularly in the Egegik River, to see where marked fish are recovered. This could help elucidate exactly where anadromous migrations may take them, and give us an idea into the dynamics of char stock structure in the Bristol Bay region. This would

likely require tagging many fish because recaptures would likely be few. I would speculate that we would find the Arctic char and Dolly Varden of the Becharof drainage part of an open population that can move freely to other systems, but with a central tendency for these fish to remain or return to this system.

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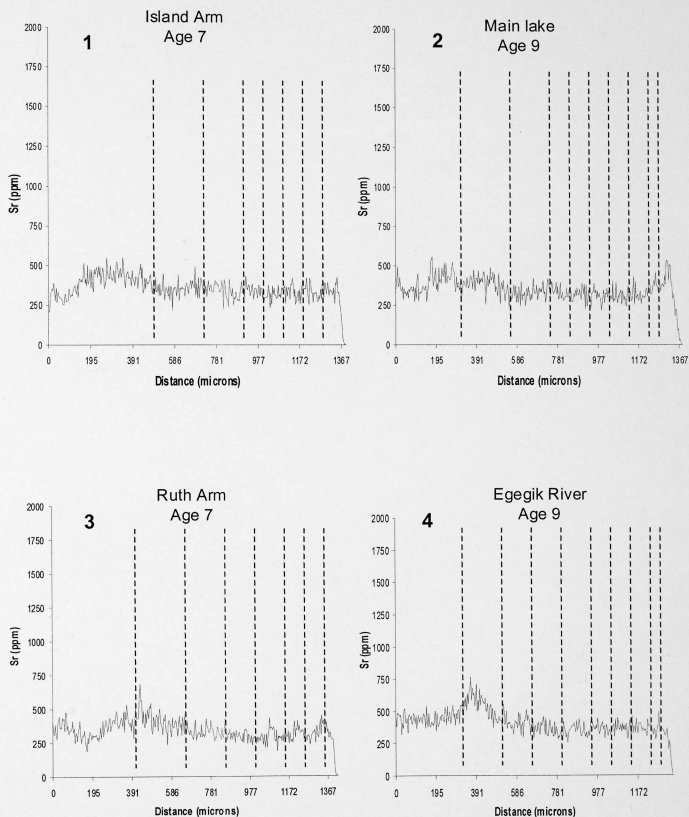
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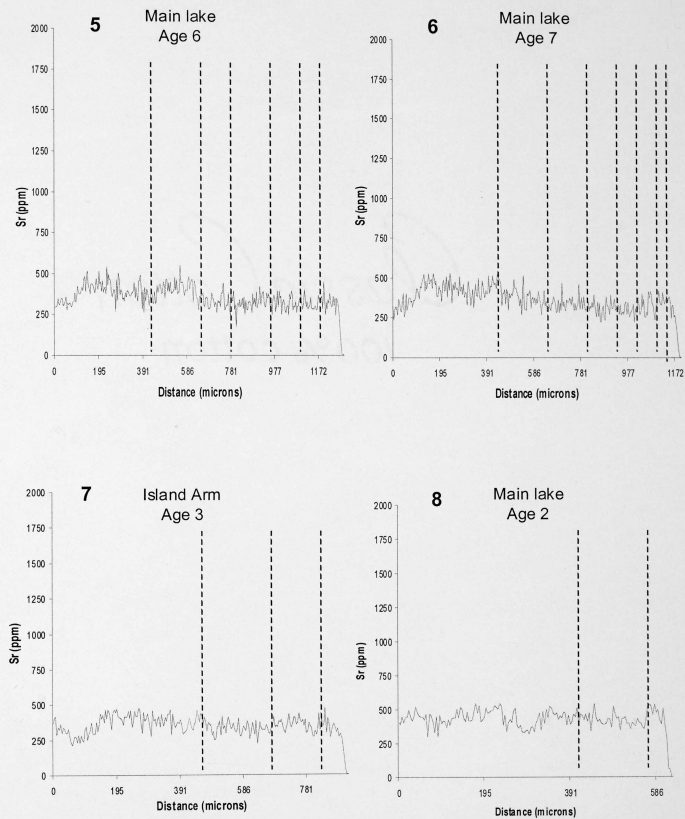
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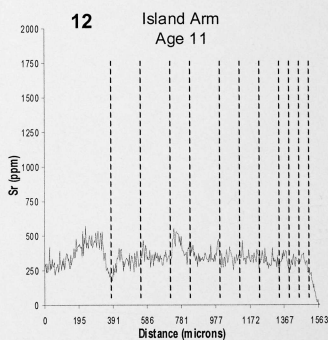
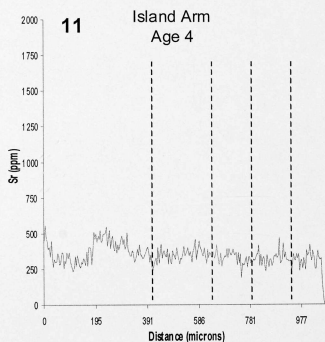
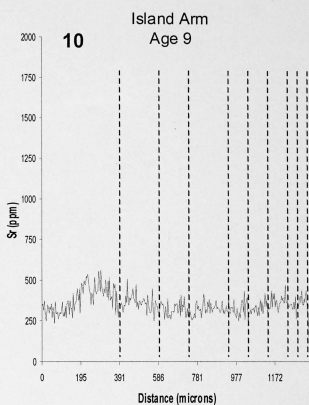
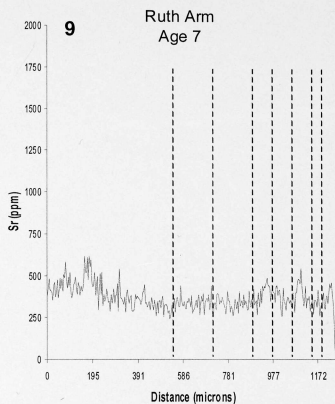
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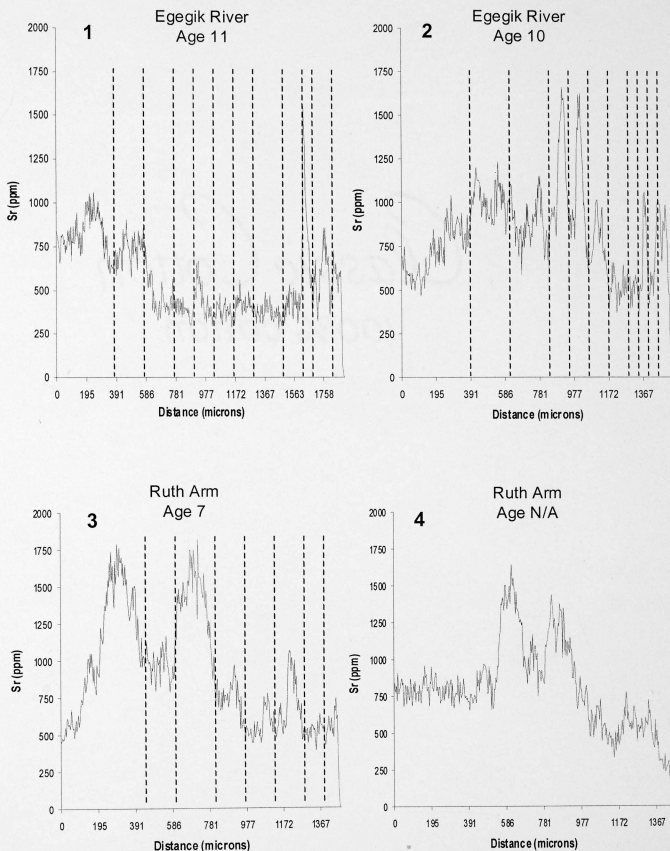
Appendix A. Line scans from twelve non-anadromous Arctic char, with locations caught and ages at capture (dashed lines denote annuli).



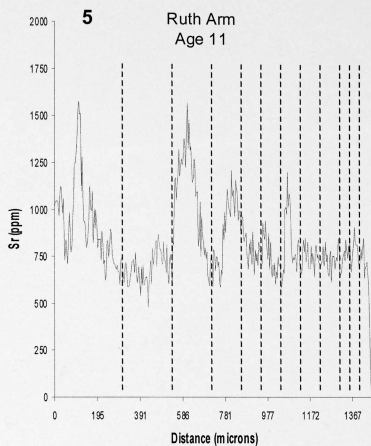
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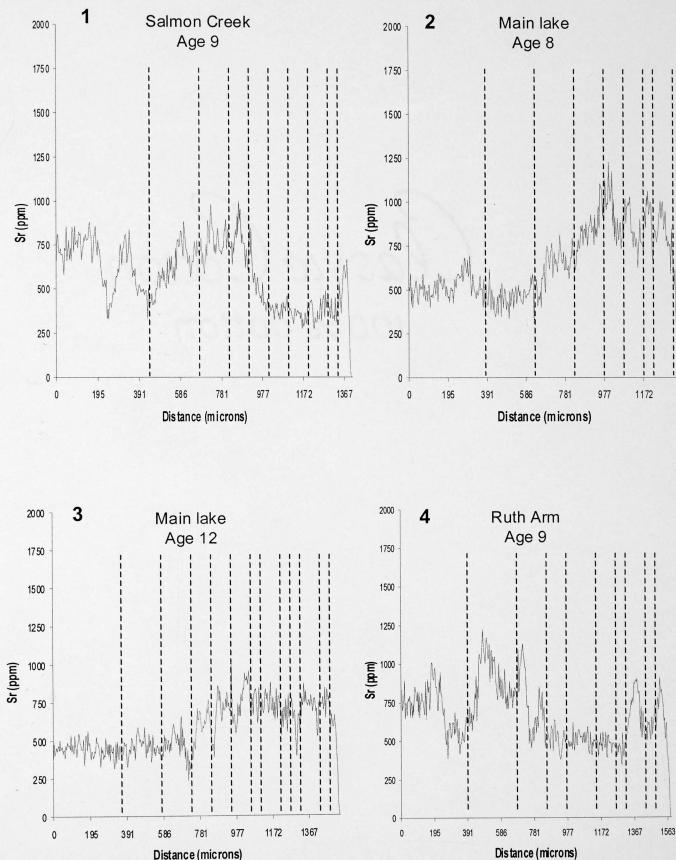
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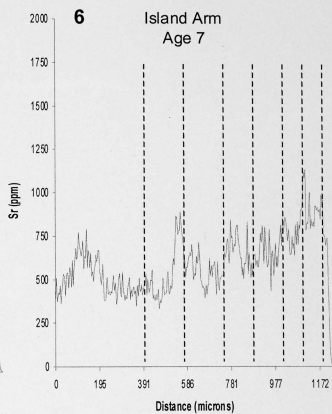
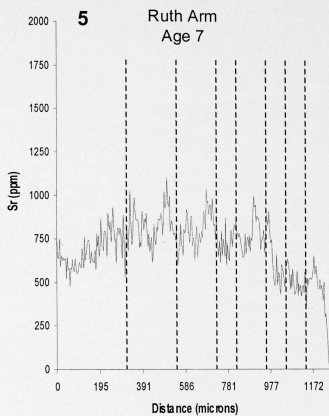
Appendix B. Line scans from five anadromous Arctic char, with locations caught and ages at capture (dashed lines denote annuli).



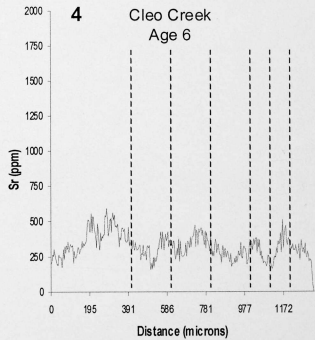
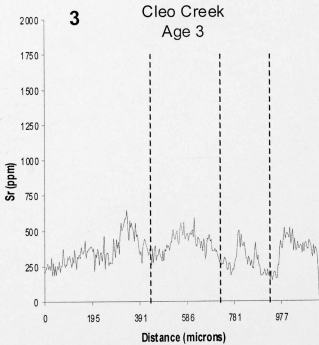
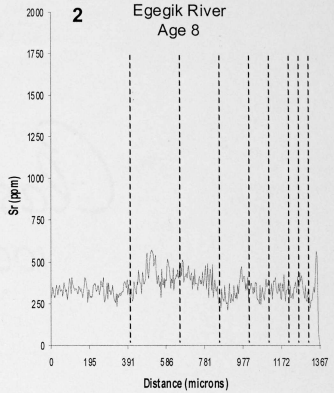
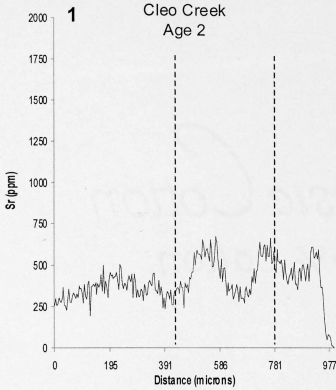
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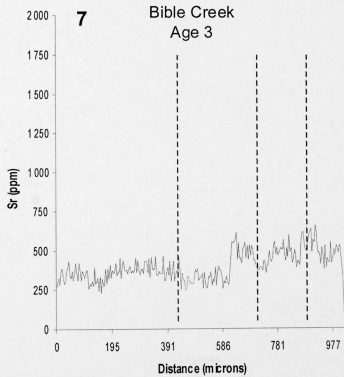
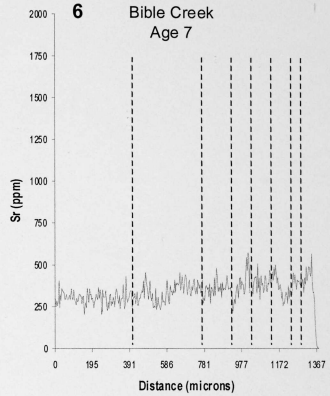
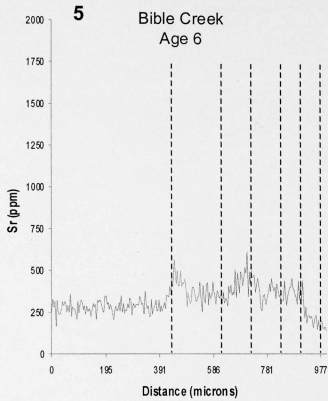
Appendix C. Line scans from six Arctic char that are difficult to interpret with respect to anadromy, with locations caught and ages at capture (dashed lines denote annuli).



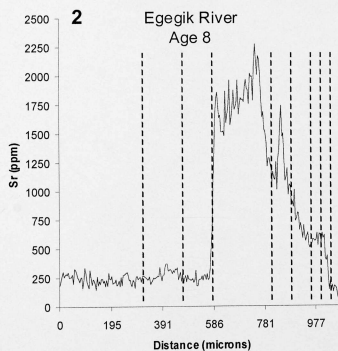
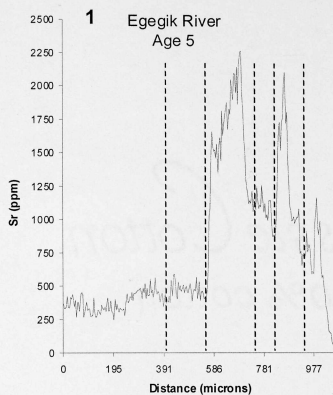
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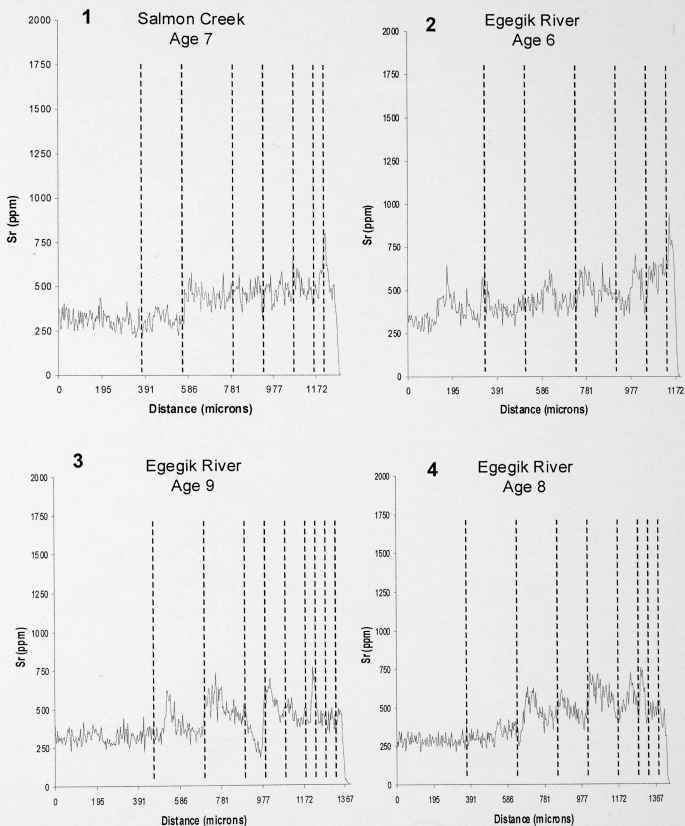
Appendix D. Line scans from seven non-anadromous Dolly Varden, with locations caught and ages at capture (dashed lines denote annuli).



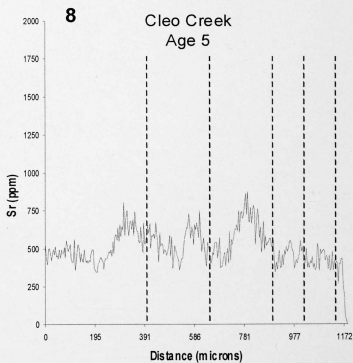
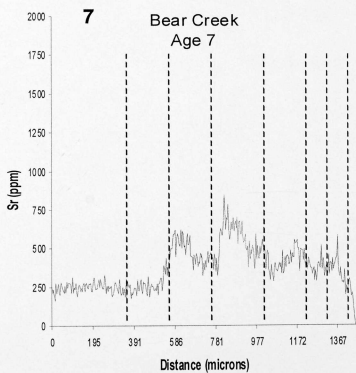
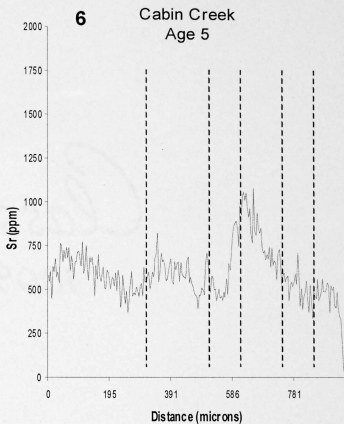
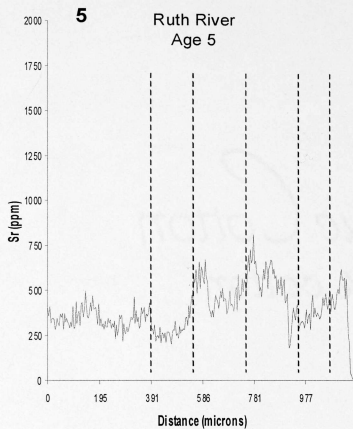
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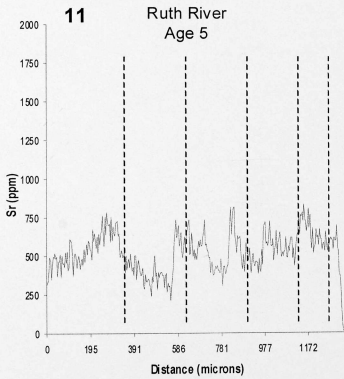
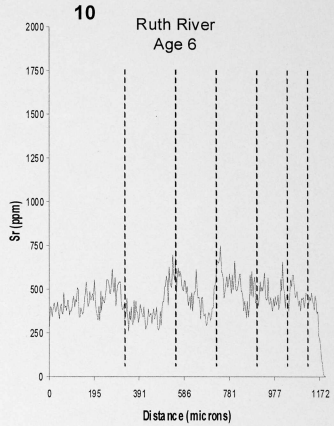
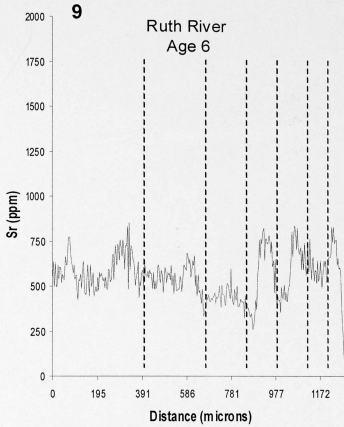
Appendix E. Line scans from two anadromous Dolly Varden, with locations caught and ages at capture (dashed lines denote annuli).



Appendix F. Line scans from eleven Dolly Varden that are difficult to interpret with respect to anadromy, with locations caught and ages at capture (dashed lines denote annuli).



Appendix F continued.



Appendix F continued.

Appendix Table A. Becharof Lake Arctic char capture history and biological information for 1998 field season.

I.D.	Capture date	Location	Water depth (m)	Fork length (mm)	Weight (kg)	Age (years)	Stomach contents	Anadromy?
E-1	19 May	Egegik River	1-2	575	1.3	12	empty	no
E-3	19 May	Egegik River	1-2	648	2.2	12	isopods, unknown fish	yes
E-8	20 May	Egegik River	1-2	684	3.8	15	nine-spined sticklebacks	N/A
E-10	20 May	Egegik River	1-2	673	2.6	10	isopod	yes
E-11	20 May	Egegik River	1-2	615	2.0	10	empty	yes
E-14	21 May	Egegik River	1-2	580	1.7	9	amphipods, isopods	N/A
E-19	21 May	Egegik River	1-2	540	1.1	9	empty	mild
E-20	22 May	Egegik River	1-2	606	2.0	10	isopods	yes
E-21	22 May	Egegik River	1-2	660	2.3	10	small fish eggs, isopods	N/A
E-24	23 May	Egegik River	1-2	625	1.6	11	small fish eggs	N/A
E-25	23 May	Egegik River	1-2	549	1.2	13	unknown fish, isopods	N/A
E-27	24 May	Egegik River	1-2	550	1.2	14	unknown fish	N/A
E-28	24 May	Egegik River	1-2	630	2.8	9	isopods	N/A
E-29	24 May	Egegik River	1-2	598	1.8	8	unknown fish	N/A
E-30	24 May	Egegik River	1-2	596	1.7	9	unknown fish	N/A
E-31	24 May	Egegik River	1-2	630	2.5	13	unknown fish	N/A
E-33	24 May	Egegik River	1-2	523	1.2	13	empty	N/A

Appendix Table A, continued.

I.D.	Capture date	Location	Water depth (m)	Fork length (mm)	Weight (kg)	Age (years)	Stomach contents	Anadromy?
S-1	5 June	Island Arm	2.5-4.5	507	1.3	7	unknown fish	no
S-2	5 June	Island Arm	2.5-4.5	480	1.0	11	three-spined sticklebacks	no
S-3	5 June	Island Arm	2.5-4.5	432	1.0	unknown	unknown fish	N/A
S-4	5 June	Island Arm	2.5-4.5	403	0.8	10	empty	N/A
S-5	5 June	Island Arm	2.5-4.5	430	0.8	7	empty	N/A
S-6	5 June	Island Arm	2.5-4.5	382	0.7	9	empty	N/A
S-7	5 June	Island Arm	2.5-4.5	355	0.5	10	empty	N/A
S-8	5 June	Island Arm	2.5-4.5	343	0.4	4	nine-spined sticklebacks	no
S-9	5 June	Island Arm	2.5-4.5	269	0.2	unknown	empty	N/A
S-10	6 June	Island Arm	19	430	0.8	7	empty	N/A
S-11	6 June	Island Arm	19	410	0.7	6	empty	N/A
S-12	6 June	Island Arm	19	466	1.2	7	isopods	N/A
S-13	6 June	Island Arm	19	330	0.3	5	unknown fish	N/A
S-14	6 June	Island Arm	19	314	0.3	3	nine-spined sticklebacks	N/A
S-15	6 June	Island Arm	2.5-4.5	392	0.7	7	nine-spined sticklebacks	N/A
S-16	6 June	Island Arm	2.5-4.5	402	0.7	7	nine-spined sticklebacks	N/A
S-17	6 June	Island Arm	2.5-4.5	445	0.9	7	empty	N/A

Appendix Table A, continued.

I.D.	Capture date	Location	Water depth (m)	Fork length (mm)	Weight (kg)	Age (years)	Stomach contents	Anadromy?
S-18	6 June	Island Arm	2.5-4.5	455	1.0	9	three-spined sticklebacks	no
S-19	6 June	Island Arm	2.5-4.5	478	1.2	6	unknown fish	N/A
S-20	6 June	Island Arm	2.5-4.5	396	0.7	5	nine-spined sticklebacks	N/A
S-21	8 June	Island Arm	5-10	520	1.4	9	nine-spined sticklebacks	N/A
S-22	8 June	Island Arm	5-10	350	0.5	8	empty	N/A
S-23	8 June	Island Arm	5-10	395	0.7	6	nine-spined sticklebacks	N/A
S-24	8 June	Island Arm	5-10	495	1.2	6	empty	N/A
S-25	8 June	Island Arm	5-10	366	0.5	unknown	unknown fish	N/A
S-26	8 June	Island Arm	5-10	360	0.5	4	nine-spined sticklebacks	N/A
S-27	8 June	Island Arm	5-10	425	0.6	5	nine-spined sticklebacks	N/A
S-28	8 June	Island Arm	5-10	455	0.9	4	snails	N/A
S-29	9 June	Ruth Arm	2	466	1.3	11	snails	yes
S-30	9 June	Ruth Arm	2	451	0.7	unknown	empty	N/A
S-31	9 June	Ruth Arm	2	462	1.2	8	pygmy whitefish	N/A
S-32	9 June	Ruth Arm	2	471	1.1	unknown	nine-spined stickleback, isopod	yes
S-33	9 June	Ruth Arm	2	470	1.1	7	unknown fish	mild

Appendix Table A, continued.

I.D.	Capture date	Location	Water depth (m)	Fork length (mm)	Weight (kg)	Age (years)	Stomach contents	Anadromy?
S-34	9 June	Ruth Arm	2	552	1.4	7	isopods	yes
S-51	11 June	Island Arm	25	252	0.2	3	unknown fish	N/A
S-52	11 June	Island Arm	25	271	0.2	4	pygmy whitefish	N/A
S-53	11 June	Island Arm	25	295	0.2	3	empty	N/A
S-54	11 June	Island Arm	25	283	0.2	4	pygmy whitefish	N/A
S-55	11 June	Island Arm	25	276	0.3	3	isopod	N/A
S-56	11 June	Island Arm	25	282	0.2	unknown	unknown fish	N/A
S-57	11 June	Island Arm	25	294	0.3	5	isopods	N/A
S-58	11 June	Island Arm	25	270	0.2	2	empty	N/A
S-59	11 June	Island Arm	25	336	0.3	3	empty	N/A
S-60	11 June	Island Arm	25	255	0.2	unknown	empty	N/A
S-61	11 June	Island Arm	25	304	0.3	3	empty	N/A
S-62	11 June	Island Arm	25	363	0.5	10	isopods	N/A
S-63	11 June	Island Arm	25	380	unknown	7	unknown fish	N/A
S-64	11 June	Island Arm	25	352	0.5	7	empty	N/A
S-65	11 June	Island Arm	25	475	0.8	9	unknown fish	N/A

Appendix Table A, continued.

I.D.	Capture date	Location	Water depth (m)	Fork length (mm)	Weight (kg)	Age (years)	Stomach contents	Anadromy?
S-66	11 June	Island Arm	25	396	0.5	5	empty	N/A
S-67	11 June	Island Arm	25	385	0.6	7	nine-spined stickleback	N/A
S-68	16 June	main lake	45	418	0.7	unknown	dipterans, isopods	N/A
S-69	16 June	main lake	45	445	0.8	unknown	dipterans	N/A
S-70	16 June	main lake	45	216	0.1	5	dipterans	N/A
S-71	16 June	main lake	45	463	0.9	9	unk. stickleback, dipterans, isopods	N/A
S-72	16 June	main lake	45	290	0.1	4	dipterans	N/A
S-73	16 June	main lake	45	367	0.5	3	dipterans	N/A
S-74	16 June	main lake	45	450	0.9	unknown	dipterans	N/A
S-75	16 June	main lake	45	450	1.0	6	dipterans, isopods	N/A
S-76	16 June	main lake	45	430	0.8	6	dipterans	N/A
S-77	16 June	main lake	45	445	0.9	7	dipterans	no
S-78	18 June	Island Arm	1-3	570	2.4	unknown	juvenile cohos	N/A
S-79	20 June	Ruth Arm	1-2	545	1.6	9	unknown fish, isopods	mild
S-80	20 June	Ruth Arm	1-2	560	1.7	10	empty	N/A
S-81	20 June	Ruth Arm	1-2	602	2.5	9	unknown fish, isopods	N/A
S-82	20 June	Ruth Arm	1-2	373	0.6	unknown	isopods	N/A

Appendix Table A, continued.

I.D.	Capture date	Location	Water depth (m)	Fork length (mm)	Weight (kg)	Age (years)	Stomach contents	Anadromy?
S-83	20 June	Ruth Arm	1-2	430	0.9	7	unknown fish	no
S-84	25 June	main lake	1-12	590	2.2	11	three-spined stickleback	N/A
S-85	25 June	main lake	1-12	440	0.8	7	empty	N/A
S-86	25 June	main lake	1-12	500	1.2	13	unknown fish, trichopterans	N/A
S-87	25 June	main lake	1-12	415	0.7	10	unknown fish	N/A
S-88	25 June	main lake	1-12	440	0.8	6	unknown fish	no
S-89	25 June	main lake	1-12	400	0.7	6	trichopterans	N/A
S-90	25 June	main lake	1-12	208	unknown	3	small isopods	N/A
S-91	25 June	main lake	1-12	129	unknown	2	juvenile salmon	N/A
S-93	25 June	main lake	1-12	104	unknown	2	trichopterans	no
S-94	28 June	main lake	80-100	380	0.7	5	juvenile sockeye	N/A
S-95	28 June	main lake	80-100	323	0.3	6	unknown fish	N/A
S-108	29 June	Island Arm	25	203	0.2	3	empty	no
S-109	29 June	Island Arm	25	201	0.1	unknown	snail	N/A
S-110	29 June	Island Arm	25	196	0.1	4	empty	N/A
S-111	29 June	Island Arm	25	211	0.2	4	unknown fish	N/A

Appendix Table A, continued.

I.D.	Capture date	Location	Water depth (m)	Fork length (mm)	Weight (kg)	Age (years)	Stomach contents	Anadromy?
S-112	29 June	Island Arm	25	215	0.1	5	unknown fish, isopods	N/A
S-113	29 June	Island Arm	25	202	0.1	4	empty	N/A
S-114	29 June	Island Arm	25	202	0.1	4	unknown fish	N/A
S-115	29 June	Island Arm	25	196	0.1	unknown	isopods	N/A
S-116	29 June	Island Arm	25	202	0.1	7	empty	N/A
S-117	29 June	Island Arm	25	188	0.1	unknown	isopods	N/A
S-118	1 July	Island Arm	35-45	520	1.7	13	isopods	N/A
S-119	1 July	Island Arm	35-45	252	0.2	6	unknown fish	N/A
S-120	1 July	Island Arm	35-45	320	0.4	7	empty	N/A
S-121	1 July	Island Arm	35-45	350	0.5	5	nine-spined stickleback	N/A
S-122	1 July	Island Arm	35-45	400	0.7	6	nine-spined stickleback	N/A
S-123	1 July	Island Arm	35-45	351	0.5	6	nine-spined stickleback	N/A
S-124	1 July	Island Arm	35-45	290	0.3	5	unknown fish	N/A
S-125	1 July	Island Arm	35-45	295	0.3	6	isopods	N/A
S-126	1 July	Island Arm	35-45	242	0.2	4	empty	N/A
S-127	1 July	Island Arm	35-45	350	0.5	5	sculpins	N/A

Appendix Table A, continued.

I.D.	Capture date	Location	Water depth (m)	Fork length (mm)	Weight (kg)	Age (years)	Stomach contents	Anadromy?
S-128	1 July	Island Arm	35-45	368	0.5	7	sculpins	N/A
S-129	1 July	Island Arm	35-45	330	0.4	5	isopods	N/A
S-130	1 July	Island Arm	35-45	314	0.4	5	nine-spined stickleback	N/A
S-131	1 July	Island Arm	35-45	210	0.2	2	isopods	N/A
S-132	1 July	Island Arm	35-45	273	0.2	unknown	empty	N/A
S-133	1 July	Island Arm	35-45	204	0.1	2	empty	N/A
S-134	1 July	Island Arm	35-45	228	0.2	2	empty	N/A
F-3	11 August	Island Arm	22-25	355	0.5	8	nine-spined stickleback	N/A
F-4	11 August	Island Arm	22-25	520	2.0	unknown	isopods, snails	N/A
F-5	11 August	Island Arm	22-25	530	1.8	11	isopods	N/A
F-6	11 August	Island Arm	22-25	442	0.9	6	empty	mild
F-7	11 August	Island Arm	22-25	370	0.6	10	nine-spined stickleback	N/A
F-8	11 August	Island Arm	22-25	405	0.7	6	nine-spined stickleback, isopod	N/A
F-9	11 August	Island Arm	22-25	375	0.7	9	nine-spined stickleback	N/A
F-10	11 August	Island Arm	22-25	295	0.3	5	nine-spined stickleback	N/A
F-11	13 August	Island Arm	2-4	127	0.1	1-2	empty	N/A
F-12	13 August	Island Arm	2-4	585	1.9	13	empty	mild

Appendix Table A, continued.

I.D.	Capture date	Location	Water depth (m)	Fork length (mm)	Weight (kg)	Age (years)	Stomach contents	Anadromy?
F-13	14 August	main lake	13-23	500	1.5	13	isopods	N/A
F-14	14 August	main lake	13-23	502	1.0	7	isopods	N/A
F-15	14 August	main lake	13-23	308	0.3	9	pygmy whitefish	N/A
F-16	14 August	main lake	13-23	580	2.3	9	isopods	yes
F-17	14 August	main lake	13-23	530	1.8	9	isopods	mild
F-18	14 August	main lake	13-23	493	1.3	8	isopods	N/A
F-19	14 August	main lake	13-23	564	2.0	14	isopods	yes
F-20	14 August	main lake	13-23	510	1.5	12	isopods, sockeye eggs	N/A
F-21	14 August	main lake	13-23	494	1.1	9	isopods	no
F-22	14 August	main lake	13-23	385	0.6	7	isopods	N/A
F-23	14 August	main lake	13-23	438	0.7	10	unknown fish	N/A
F-24	14 August	main lake	13-23	380	0.5	8	empty	N/A
F-25	14 August	main lake	13-23	404	0.6	5	unknown fish	N/A
F-26	14 August	main lake	13-23	345	0.4	7	empty	N/A
F-27	14 August	main lake	13-23	285	0.2	unknown	isopods	N/A
F-28	15 August	main lake	53-68	222	0.1	4	pygmy whitefish	N/A
F-29	15 August	main lake	53-68	384	0.5	unknown	empty	N/A

Appendix Table A, continued.

I.D.	Capture date	Location	Water depth (m)	Fork length (mm)	Weight (kg)	Age (years)	Stomach contents	Anadromy?
F-41	24 August	Egegik River	1-2	519	1.0	8	sockeye egg, isopod	N/A
F-45	28 August	Island Arm	4-7	493	1.5	11	snails	N/A
F-46	28 August	Island Arm	4-7	434	1.2	7	isopods	N/A
F-47	28 August	Island Arm	4-7	363	0.6	7	isopods, dipterans	N/A
F-48	28 August	Island Arm	4-7	258	0.2	4	isopods	N/A
F-49	28 August	Island Arm	4-7	209	0.1	4	isopods	N/A
F-54	31 August	Island Arm	10-14	479	0.8	9	three-spined sticklebacks	N/A
F-55	31 August	Island Arm	10-14	186	0.1	3	empty	N/A
F-56	31 August	Island Arm	10-14	176	0.1	2	empty	N/A
F-57	31 August	main lake	80-100	505	1.0	10	nine-spined sticklebacks	N/A
F-58	31 August	main lake	80-100	494	0.8	9	sockeye juvenile, isopod	N/A
F-60	2 September	Island Arm	40	466	1.1	7	nine-spined sticklebacks	no
F-61	2 September	Island Arm	40	426	0.9	8	dipterans	N/A
F-62	2 September	Island Arm	40	385	0.8	7	isopods	N/A
F-63	2 September	Island Arm	40	270	0.2	5	three-spined sticklebacks	N/A
F-64	2 September	Island Arm	40	375	0.6	9	empty	N/A
F-65	2 September	Island Arm	40	397	0.8	11	juvenile sockeye, isopods	N/A

Appendix Table A, continued.

I.D.	Capture date	Location	Water depth (m)	Fork length (mm)	Weight (kg)	Age (years)	Stomach contents	Anadromy?
F-66	2 September	Island Arm	40	518	1.5	10	isopods	N/A
F-67	2 September	Island Arm	40	384	0.6	unknown	unknown fish	N/A
F-68	2 September	Island Arm	40	395	0.7	8	juvenile sockeye	N/A
F-69	2 September	Island Arm	40	324	0.5	4	isopods	N/A
F-70	2 September	Island Arm	40	302	0.3	4	three- and nine-spined sticklebacks	N/A
F-71	2 September	Island Arm	40	371	0.5	7	juvenile sockeye	N/A
F-72	2 September	Island Arm	40	324	0.4	5	unknown fish	N/A
F-73	2 September	Island Arm	40	304	0.4	3	nine-spined sticklebacks	N/A
F-74	2 September	Island Arm	40	351	0.5	7	nine-spined sticklebacks	N/A
F-75	2 September	Island Arm	40	253	0.2	unknown	unknown fish	N/A
F-76	2 September	Island Arm	40	276	0.3	6	juvenile sockeye	N/A
F-77	2 September	Island Arm	40	231	0.2	3	juvenile sockeye	N/A
F-78	2 September	Island Arm	40	235	0.2	5	unknown fish	N/A
F-79	7 September	Ruth Lake	2-5	479	1.3	10	isopods	N/A
F-80	7 September	Ruth Lake	2-5	320	0.4	7	isopods	N/A
F-81	7 September	Ruth Lake	2-5	362	0.6	8	nine-spined sticklebacks	N/A
F-82	7 September	Ruth Lake	2-5	344	0.5	7	sockeye eggs	N/A

Appendix Table A, continued.

<u>I.D.</u>	<u>Capture date</u>	<u>Location</u>	<u>Water depth (m)</u>	<u>Fork length (mm)</u>	<u>Weight (kg)</u>	<u>Age (years)</u>	<u>Stomach contents</u>	<u>Anadromy?</u>
F-83	8 September	Salmon Creek	1	458	0.7	9	sockeye egg, isopods	mild

Appendix Table B. Becharof Lake Dolly Varden capture history and biological information for 1998 field season.

I.D.	Capture date	Location	Water depth (m)	Fork length (mm)	Weight (kg)	Age (years)	Stomach contents	Anadromy?
E-2	19 May	Egegik River	1-2	545	1.2	12	dipterans	no
E-4	19 May	Egegik River	1-2	533	1.0	8	dipterans	mild
E-5	19 May	Egegik River	1-2	490	0.8	5	empty	yes
E-6	19 May	Egegik River	1-2	427	0.7	6	dipterans, plant matter	N/A
E-7	19 May	Egegik River	1-2	473	1.1	14	dipterans, isopod	N/A
E-9	20 May	Egegik River	1-2	545	1.5	9	dipterans	mild
E-12	20 May	Egegik River	1-2	510	1.2	11	dipterans, isopods	N/A
E-13	20 May	Egegik River	1-2	440	0.9	7	isopod	N/A
E-15	21 May	Egegik River	1-2	505	0.9	7	dipterans, coleopterans	N/A
E-16	21 May	Egegik River	1-2	467	0.9	6	isopods	mild
E-17	21 May	Egegik River	1-2	602	1.3	6	dipterans	N/A
E-18	21 May	Egegik River	1-2	512	1.1	9	small gray eggs (sculpin/grayling?)	mild
E-22	22 May	Egegik River	1-2	512	1.2	7	dipterans, coleopterans	N/A
E-23	23 May	Egegik River	1-2	405	0.6	10	dipterans	N/A
E-26	23 May	Egegik River	1-2	460	0.8	6	isopods	N/A
E-32	24 May	Egegik River	1-2	432	0.7	unknown	dipterans, isopods	N/A
S-35	9 June	Ruth River	1-2	507	1.3	5	empty	N/A

Appendix Table B, continued.

I.D.	Capture date	Location	Water depth (m)	Fork length (mm)	Weight (kg)	Age (years)	Stomach contents	Anadromy?
S-36	9 June	Ruth River	1-2	421	0.8	6	empty	N/A
S-37	9 June	Ruth River	1-2	475	1.2	5	trichopterans	mild
S-38	9 June	Ruth River	1-2	421	0.9	7	empty	N/A
S-39	9 June	Ruth River	1-2	458	1.0	unknown	empty	N/A
S-40	9 June	Ruth River	1-2	359	0.5	unknown	unidentifiable	mild
S-41	9 June	Ruth River	1-2	370	0.5	5	dipterans, small clam	N/A
S-42	9 June	Ruth River	1-2	423	0.8	5	trichopterans	mild
S-43	9 June	Ruth River	1-2	370	0.6	unknown	empty	N/A
S-44	9 June	Ruth River	1-2	426	0.8	6	trichopterans	N/A
S-45	9 June	Ruth River	1-2	450	1.1	6	unknown insect	mild
S-46	9 June	Ruth River	1-2	455	1.1	5	empty	N/A
S-47	9 June	Ruth River	1-2	405	0.8	5	dipterans	N/A
S-48	9 June	Ruth River	1-2	446	0.9	6	empty	mild
S-49	9 June	Ruth River	1-2	495	1.2	6	empty	N/A
S-50	9 June	Ruth River	1-2	502	1.2	8	empty	N/A
S-92	25 June	main lake	1-12	124	unknown	1-2	empty	N/A
S-96	28 June	Cleo Creek	1	443	0.8	5	trichopterans	N/A

Appendix Table B, continued.

I.D.	Capture date	Location	Water depth (m)	Fork length (mm)	Weight (kg)	Age (years)	Stomach contents	Anadromy?
S-97	28 June	Cleo Creek	1	unknown	1.3	unknown	isopods	N/A
S-98	29 June	Bear Creek	1-2	542	1.7	7	empty	N/A
S-99	29 June	Bear Creek	1-2	500	1.4	7	empty	N/A
S-100	29 June	Bear Creek	1-2	374	0.5	3	trichopterans	N/A
S-101	29 June	Bear Creek	1-2	478	1.3	5	empty	no
S-102	29 June	Bear Creek	1-2	380	0.6	unknown	trichopterans, coleopterans	N/A
S-103	29 June	Bear Creek	1-2	460	1.1	5	empty	N/A
S-104	29 June	Bear Creek	1-2	500	1.9	5	empty	N/A
S-105	29 June	Bear Creek	1-2	485	1.4	7	coleopterans	mild
S-106	29 June	Bear Creek	1-2	494	1.3	6	empty	N/A
S-107	29 June	Bear Creek	1-2	488	1.3	6	empty	N/A
S-135	2 July	Featherly Creek	1-2	447	0.9	5	unk. fish, trichopterans, dipterans	no
S-136	3 July	Cleo Creek	1	507	1.1	5	empty	N/A
S-137	5 July	Cabin Creek	1	448	0.9	5	unk. eggs, trichopterans, coleopterans	no
S-138	8 July	Cleo Creek	1	370	0.5	5	trichopterans, coleopterans	N/A
S-139	8 July	Cleo Creek	1	132	unknown	1-2	empty	N/A

Appendix Table B, continued.

I.D.	Capture date	Location	Water depth (m)	Fork length (mm)	Weight (kg)	Age (years)	Stomach contents	Anadromy?
F-1	10 August	Bear Creek	1-2	440	1.0	unknown	sockeye eggs	N/A
F-2	10 August	Bear Creek	1-2	497	1.1	7	sockeye eggs	N/A
F-30	15 August	Bible Creek	1	320	0.3	5	sockeye eggs	N/A
F-31	15 August	Bible Creek	1	312	0.3	3	sockeye eggs	no
F-32	15 August	Bible Creek	1	520	1.3	7	sockeye eggs	no
F-33	15 August	Bible Creek	1	470	1.2	7	sockeye eggs	no
F-34	15 August	Bible Creek	1	480	1.0	6	sockeye eggs	no
F-35	20 August	Cleo Creek	1	554	1.6	9	gravel	N/A
F-36	20 August	Cleo Creek	1	538	1.5	6	sockeye eggs, gravel	N/A
F-37	20 August	Cleo Creek	1	466	1.1	6	gravel	N/A
F-38	20 August	Cleo Creek	1	525	1.4	5	gravel	mild
F-39	20 August	Cleo Creek	1	450	0.9	3	sockeye eggs	no
F-40	21 August	Becharof Creek	1-2	578	2.0	6	sockeye eggs	N/A
F-42	24 August	Egegik River	1-2	527	1.2	8	isopod, large fish jawbone	no
F-43	27 August	Salmon Creek	1	455	0.6	4	sockeye eggs	N/A
F-44	27 August	Salmon Creek	1	494	1.2	7	sockeye eggs	mild
F-50	28 August	Cleo Creek	1	314	0.4	3	sockeye eggs	no

Appendix Table B, continued.

I.D.	Capture date	Location	Water depth (m)	Fork length (mm)	Weight (kg)	Age (years)	Stomach contents	Anadromy?
F-51	28 August	Cleo Creek	1	498	1.5	8	gravel	N/A
F-52	28 August	Cleo Creek	1	377	0.6	4	sockeye eggs	N/A
F-53	28 August	Cleo Creek	1	417	0.8	6	empty	N/A
F-59	1 September	Burls Creek	1	452	1.1	9	sockeye eggs	N/A